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CONTENTS OF VOLUME 115, NUMBER 1/2

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PROCEEDINGS

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PEER REVIEWED PAPERS

A REVIEW OF NEMATOPHAGY BY TERRESTRIAL TARDIGRADES WITH NEW OBSERVATIONS ON SOME AUSTRALIAN SPECIES

BRIAN MACKNESS

School of Biological Sciences, University of New South Wales, New South Wales 2054, Australia
Current address: PO Box 560, Beerwah, Queensland 4519, Australia

MACKNESS, B.S., 2003:06:15. A review of nematophagy by terrestrial tardigrades with new observations on some Australian species. *Proceedings of the Royal Society of Victoria* 115(1): 1-5. ISSN 0035-9211.

A literature review of nematophagy by terrestrial tardigrades was undertaken including a survey of 93 species of the genus *Macrobiotus* to determine whether there were any morphological criteria common to all nematophagous species. Preliminary results suggest that all nematophagous species have buccal tube widths greater than 17% of the tube length and that they also possess peribuccal lamellae. Two new nematophagous tardigrades, *Macrobiotus hieronimi* Pilato & Claxton, 1988 and *M. peteri* Pilato et al., 1989 have been recognized as well as further records of nematode predation by tardigrades from Australia.

Key words: Tardigrades, nematophagy, buccal tubes, peribuccal lamellae

TERRESTRIAL tardigrades are primarily vegetarian, although some are known to take animal food including nematodes (Ramazzotti & Maucci 1983). There are few reports of nematophagy however found in the literature. Linford & Oliveira (1938) reported three predacious tardigrades (*Macrobiotus* spp.) attacking root-knot nematodes *Heterodera* sp. (now various species of *Meliodogyne*). Le Gros (1958) stated that tardigrades attacked nematodes in addition to rotifers and other tardigrades. Hutchinson & Streu (1960) reported an unidentified tardigrade feeding on the nematodes *Trichodorus* sp. and *Tylenchus* sp. in the United States and in Sri Lanka. Doncaster & Hooper (1961) and Doncaster (1962) recorded *Macrobiotus richtersi* Murray, 1911 piercing nematodes and suggested that a toxin might have been secreted to immobilize large nematodes such as mononchids. Esser (1963) and Esser & Sobers (1964) examined the possibility of tardigrades being used as biological control agents of nematodes. Macrobiotid tardigrades, in citrus orchards, have been recorded feeding on the nematodes *Tylenchulus* sp. and *Meloidogyne* sp. (Boosalis & Manakau 1965, Stirling & Mankau 1977).

Sayre (1969) cultured the tardigrade *Hypsibius* (=*Isohypsibius*) *myrops* (Du Bois-Reymond Marcus, 1944) on nematodes for several months. He also observed individuals feeding on the plant nematodes *Meloidogyne* sp. and *Ditylenchus* sp. Hallas & Yeates (1972) recorded *Macrobiotus harmsworthi* Murray, 1907 feeding on nematodes and reported a strong correlation between total number of nematodes and monthly tardigrade populations. Hallas & Yates (1972) also suggested that *Hypsibius* (*I.*) *myrops* (*sensu* Sayre 1969) might be identical to *Hypsibius* (*I.*) *prosostomus*, which they also reported feeding on nematodes.

Several other authors have reported general incidents of predation by tardigrades (Cayrol 1976, Morgan 1977, Small 1988). Further investigations of predation by tardigrades were undertaken by Sayre & Wergin (1979) using a scanning electron microscope. Esser (1990) summarized more than 25 years of observing nematodes and tardigrades. These observations primarily concerned hypsibiid tardigrades feeding on a variety of nematodes. Bird (1996) figured *Macrobiotus* cf. *pseudohufelandi* Iharos, 1966 eating an unidentified soil nematode.

Hallas & Yeates (1972: 289) characterized predacious tardigrades in having '... a mouth opening (oral aperture) which points directly forward, a short, wide pharyngeal tube, strongly built stylets and a large bulbus'. A survey was undertaken of published buccal tube widths of 93 species of *Macrobiotus* to ascertain whether this criterion could be used as a guide to recognizing pred-acious tardigrades. The incidence of buccal lamellae was also examined. The results of this survey are reported in Table 1. The author reports two hitherto unknown species of nematophagous tardigrades as well as further records of nematode predation by tardigrades from Australia.

Species	BTR	Length	Lamellae
M. beotiae Durante & Maucci, 1979	(25% of length)	880 µm	Yes
M. gildae Maucci & Durante Pasa, 1980	(22% of length)	500 µm	Yes
M. grandis Richters, 1911	(17% of length)	900 µm	Yes
***M. harmsworthi* Murray, 1907**	**(20% of length)**	**650 µm**	Yes
***M. hieronimi* Pilato & Claxton, 1988**	**(17% of length)**	**488 µm**	Yes
M. mauccii Pilato, 1974	(22% of length)	450 µm	Yes
***M. peteri* Pilato et al. 1989**	**(17% of length)**	**690 µm**	Yes
M. pseplus du Bois-Reymond Marcus, 1944	(17% of length)	800 µm	Yes
***M. pseudohufelandi* Iharos, 1966**	**(18% of length)**	**510 µm**	Yes
M. recens Cuenot, 1932	(21% of length)	624 µm	Yes
***M. richtersi* Murray, 1911**	**(20% of length)**	**750-1000 µm**	Yes
M. snaresensis Horning *et al.*,1978	(22% of length)	450 µm	Yes
M. spectabilis Thulin, 1928	(17% of length)	700 µm	Yes

Table 1. Species of *Macrobiotus* with buccal tube widths greater than 17% of buccal tube length. (Source Ramazzotti & Maucci 1983 and references cited in text). Known nematophagous tardigrades highlighted in bold. (BTR = Buccal tube ratio)

Feeding by tardigrades

Tardigrades have a complex series of organs associated with feeding. These include the buccal orifice, stylets, the pharynx and the oesophagus. The oral aperture can be terminal as in most macrobiotids or slightly ventral as in most hypsibids. The buccal cavity opens with a circular ring that may support a crown of buccal lamellae (Fig 1A). These allow the mouth to be applied like a sucker to prey (Ramazzotti & Maucci 1983). There are piercing organs on either side of the mouth called stylets. Their composition remains unclear although Marcus (1927) and Kaestner (1968) suggest they are calcareous. Bird (1996) has recorded marked bi-refringence of the stylets under polarized light and suggested this may be due to their inferred crystalline nature. The stylets themselves, are operated by several retracting and protracting muscles. Tardigrades use these stylets to pierce the cuticles of their prey. The buccal cavity is followed by a buccal tube that extends into the pharynx. The pharynx functions as a sucking organ and is generally ovoid in shape (Ramazzotti & Maucci 1983). Food is not masticated but passed by sucking action through a short oesophagus into the midgut where digestion takes place.

In some tardigrades, particularly Family Macrobiotidae, there is a series of circular swellings called placoids in the pharyngeal bulb (Fig 1B). They are thought to play a role in mechanical reinforcement of the pharynx (Ramazzotti & Maucci 1983). There are also large rostral or salivary glands located lateral to the buccal tube and pharyngeal bulb. It has not been confirmed whether these glands secrete digestive juices and indeed some authors, such as Cuénot (1932), have ascribed an excretory function to them.

There appears to be no pattern to the choice or size of nematode taken as prey by tardigrades (Doncaster & Hooper 1961). Tardigrades have been recorded passing within 10 µm of a nematode without any attempt to attack (Esser 1990). Likewise, not all attacks by tardigrades are successful. Esser (1990) observed an attack by a tardigrade on the nematode *Enchodelus* (three and a half times larger than the tardigrade) that was unsuccessful as well as another on a large dorylaim. Prey is normally pierced with the stylets and the body contents sucked out. Several tardigrades may attack the same nematode simultaneously (Doncaster & Hooper 1961).

Sometimes the prey is swallowed whole. Ramazzotti & Maucci (1983) observed *Macrobiotus richtersi*, with a buccal tube of 12 µm, with a whole nematode inside its stomach. Hallas & Yeates (1972) observed *M. harmsworthi* with a nematode tail projecting out of its cloaca. Apparently it had ingested the nematode tail first and the thinner posterior end had passed through the gut unruptured while the anterior end had been digested.

When tardigrade attacks occur, they can be quite rapacious and sustained. Esser & Sobers (1964: 333) reported an earlier observation by Esser of tardigrades

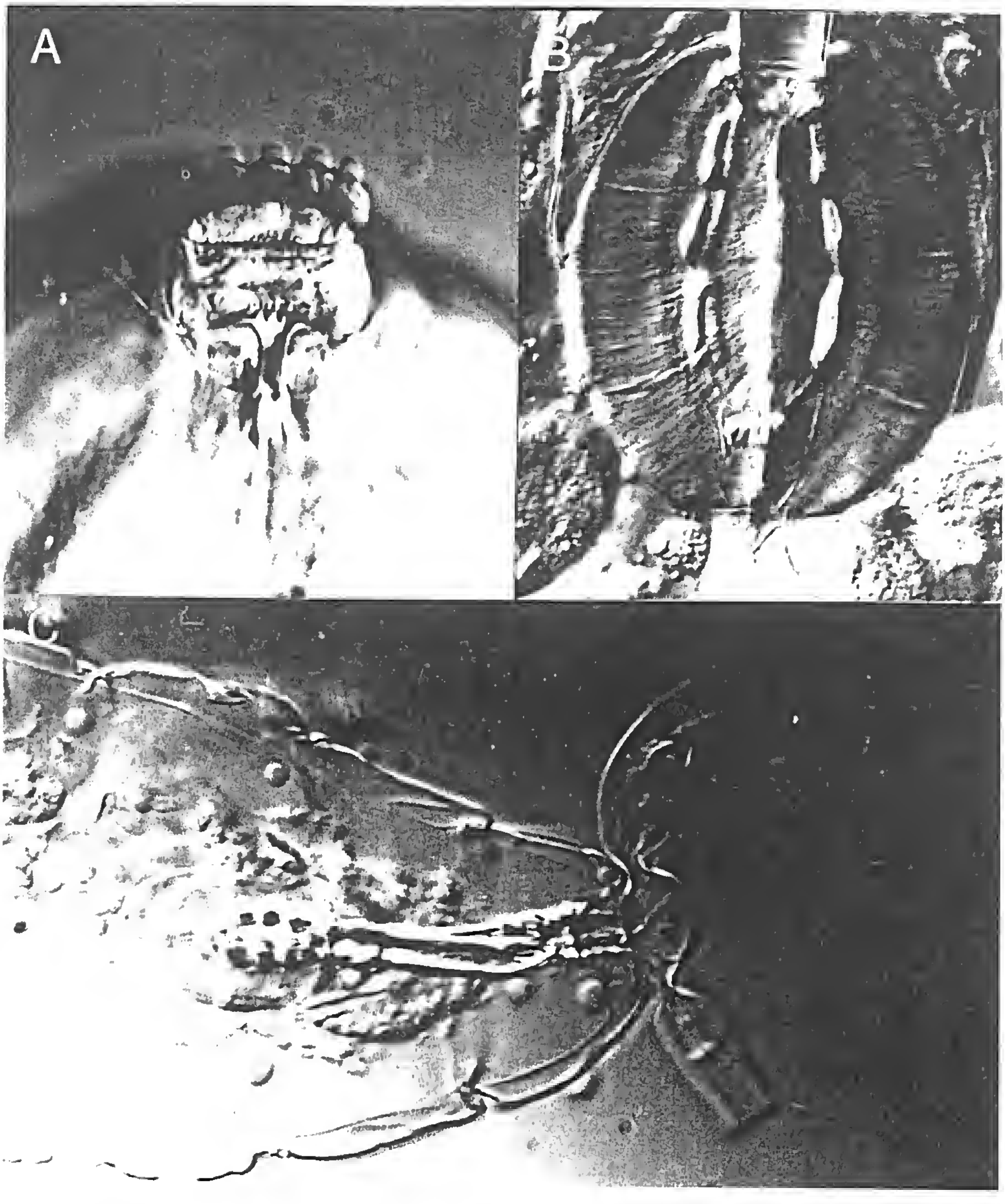

Fig. 1. A, Peribuccal lamellae at entrance to buccal cavity. B, Pharyngeal bulb with placoids. C, *Macrobiotus* sp. from Mt Ainsley, ACT with nematode. Scale bar = 100 µm

'viciously attacking nematodes, ripping many of them to pieces and swallowing some of them whole'. Hutchinson & Streu (1960) reported that tardigrades made distinct tears in the cuticles of nematodes while Esser (1990) recorded a tardigrade holding on to a nematode for over three hours. Doncaster & Hooper (1961) suggested that tardigrades might inject a toxic secretion into nematodes in order to subdue them.

The following tardigrade species from Australia and Lord Howe Island have been observed feeding on nematodes.

Macrobiotus hieronimi Pilato & Claxton, 1988

One specimen (LH3-13) collected by Jo Mon from Lord Howe Island (6/7/80) and mounted by S.K. Claxton. Tardigrade is 420 µm long and recovered from damp moss *Ptychomitrium* sp. with 25-50% moisture content. The nematode is being attacked head on and all of the pharyngeal region has been consumed and internal structures dissolved. Consequently identification of the nematode is not possible. This is the first published record of nematophagy by this species.

Macrobiotus peteri Pilato et al., 1989

Three specimens (ATS1065-3, 1067-16, 1090-10) collected and mounted by S.K. Claxton, Douglas Park, NSW. Tardigrades found in moss *Dicnemoloma* sp. The nematodes cannot be identified. Tardigrades are 320 µm, 420 µm and 430 µm long respectively. This is the first published record of nematophagy by this species.

Macrobiotus richtersi Murray, 1911

One specimen (ATS 417-1) collected and mounted by S.K. Claxton, Cedarvale, NSW from moss/lichen. The nematode cannot be identified. The tardigrade is 420 µm long.

Milnesium tardigradum Doyère, 1840

One specimen (ATS 1058-37) collected by S.K. Claxton, Cambewarra Mountains, NSW. Tardigrade found in foliose lichen *Parmotrema* sp. and is 550 µm long. The tardigrade has attacked the nematode (which appears to be a female enoplid) in the middle of the body. It has a characteristic cylindrical pharynx, the posterior portion of which has been partly digested (A. Bird pers. comm.). *Milnesium tardigradum* is an active predator of both nematodes and other tardigrades.

Macrobiotus sp. (Fig 1C)

One specimen (ATS 507/13) collected and mounted by G. Carruthers, east face of Mt Ainsley, ACT, 10 metres below summit. The tardigrade was found in wet moss and lichen. It is holding the nematode in its mouth. The body walls of the nematode are constricted at either end of the tardigrades mouth. The nematode can not be identified.

DISCUSSION

Four genera of tardigrades are known to prey on nematodes - *Milnesium*, *Macrobiotus*, *Isohypsibius* and *Hypsibius*. Six species of *Macrobiotus* have been recorded feeding on nematodes. Preliminary results of a survey of 93 macrobiotid tardigrades suggests that all nematophagous species have proportionally wider buccal tubes with widths at least 17% of buccal tube length. They also all possess buccal lamellae. Using these criteria, a further eight tardigrades may be potentially nematophagous. These are *Macrobiotus beotiae* Durante & Maucci, 1979; *M. gildae* Maucci & Durante Pasa, 1980; *M. grandis* Richters, 1911; *M. maucci* Pilato, 1974; *M. psephus* du Bois-Reymond Marcus, 1944; *M. recens* Cuénot, 1932; *M. snaresensis* Horning *et al.*, 1978 and *M. spectabilis* Thulin, 1928. Further field collecting of these potential nematophagous species is needed to test the hypothesis of Hallas & Yeates (1972) that there is a morphological basis for nematode predation by tardigrades. The width of the buccal tube is not correlated to the length of the tardigrade (Ramazzotti & Maucci 1983) nor does there seem to be any relationship between the size of the nematode being attacked and the size of the attacking tardigrade with nematodes three times larger being attacked (Esser 1990). Large vigorous nematodes may be able to squirm free although observations show that tardigrades can be quite dogged in their attempts to subdue their prey often hanging on for hours (Esser 1990).

It appears that there are many factors involved in nematode prey selection by tardigrades. Hallas & Yeates (1972) have shown a direct correlation between numbers of *Macrobiotus harmsworthi* and the availability of prey, even when environmental factors are taken into account (simple rank correlation + 0.273; moisture excluded = 0.287; temperature excluded + 0.286). When Esser (1990) placed several large populations of tardigrades on water agar containing numerous nematodes of many genera, no feeding or attacking was noted for several weeks. Esser (1990) suggested that the rarity of attacks in agar solution was because the conditions under which tardigrades feed are rarely obtained outside their normal habitat. There also appears to be no correlation between what types of nematodes are eaten by tardigrades. Bacterio-phagous, phytophagous and a variety of predacious nematodes have all been taken. One of the problems

in ascertaining what types of nematodes become prey is that the feeding action of tardigrades normally dissolves vital taxonomic features of the nematodes concerned. Tardigrade/nematode interactions occur in a variety of microhabitats and under a range of environmental conditions. Further research needs to be undertaken to understand the roles that these various factors play in both prey selection by tardigrades and the frequency and cause of attacks.

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EARLY DEVONIAN (EMSIAN) VERTEBRATE MICROREMAINS FROM THE BUCHAN GROUP, VICTORIA, AUSTRALIA

ALISON BASDEN

Centre for Ecostratigraphy and Palaeobiology, Department of Earth and Planetary Sciences, Macquarie University, New South Wales 2109, Australia

BASDEN, A., 2003:06:15. Early Devonian (Emsian) vertebrate microremains from the Buchan Group, Victoria, Australia. *Proceedings of the Royal Society of Victoria* 115(1) : 7-26. ISSN 0035-9211.

The vertebrate microfauna from the Early Devonian Buchan Group in northeastern Victoria is dominated by remains of acanthodians and placoderms, with osteichthyans less common, and chondrichthyans and thelodonts rare. Acanthodian remains include scales of *Nostolepoides platymarginata*, "*Nostolepis*" *guangxiensis*, *Gomphonchus? bogongensis*, scales similar to those of *Cheiracanthoides comptus* and *C. wangi*, and possible *Rhadinacanthus* scales. Scales of arthrodires *Goodradigbeeon* and *Buchanosteus* are the most abundant placoderm remains; placoderm plate fragments are attributed to *Buchanosteus* and *Murrindalaspis*. Osteichthyan remains include a scale of the actinopterygian *Ligulalepis toombsi*, and onychodont scales and teeth. Taxa previously undescribed from Buchan are acanthodians "*Nostolepis*" *guangxiensis*, *Cheiracanthoides* sp. cf. *C. wangi* and *Rhadinacanthus*, chondrichthyan *Ohiolepis* sp., and osteichthyan *Ligulalepis toombsi*.

Key words: Early Devonian, Emsian, vertebrate microfossil, acanthodian, placoderm, chondrichthyan, osteichthyan

DEVONIAN fossil fish remains have been known from the Buchan area of northeastern Victoria for well over a century. McCoy (1876) described as '*Asterolepis ornata* var. *australis*' a placoderm bone that has subsequently been shown to be portion of the skull of a large arthrodire (Young 1979). From the same area, an almost complete arthrodire skull was initially described by Chapman (1916), subsequently prepared in hydrochloric acid by Hills (1936) who referred it to the European genus *Coccosteus*, and eventually assigned to the new genus *Buchanosteus* by Stensiö (1945). Hills (1936) also described a mandible of the lungfish *Dipnorhynchus* from the same area.

The only recent description of macrovertebrate material from Buchan is by Long (1984a), who assigned various disarticulated plates from the McLarty Member of the Murrindal Limestone to *Buchanosteus confertituberculatus*, and described two new acanthothoracids, *Murrindalaspis wallacei* and *M. bairdi*. He identified several forms first described from the coeval Taemas/Wee Jasper fauna in southern New South Wales: brachythoracids *Arenipiscis westolli*, *Errolosteus* sp. cf. *E. goodradigbeensis*, and *Taemasosteus maclartiensis*, and petalichthyid *Wijdeaspis warrooensis*. Long (1984b) illustrated another *Buchanosteus* specimen, which included scales described by Burrow & Turner (1998, 1999). The only other vertebrate microremains known from the Buchan region are scales of the dipnoan *Dipnorhynchus* illustrated by Thomson & Campbell (1971, figs 86-88).

The Early Devonian Buchan Group at Buchan, Victoria (Emsian: *dehiscens* - *serotinus* zones) comprises three formations (Fig. 1). The Buchan Caves Limestone, predominantly calcarenites and calcisiltites with dolomites and dolomitic limestones (*dehiscens* Zone) is overlain by the nodular and impure limestones and shales of the Taravale Formation (*dehiscens* - *serotinus* zones) and the well-bedded and massive limestones with subordinate mudstones of the Murrindal Limestone (*perbonus* Zone). Detailed geology and conodont biostratigraphy were discussed by Mawson (1987) and Mawson et al. (1988, 1992).

Other studies have demonstrated the generally fossiliferous nature of these horizons, describing an invertebrate fauna of abundant stromatoporoids and corals associated with brachiopods, bivalves and ostracods in the Buchan Caves Limestone (Webby et al. 1993; Talent 1995), and more diverse faunas of brachiopods, corals, and trilobites, the oldest known ammonoids, dacryoconarids, ostracods, agglutinated foraminiferans, scolecodonts and chitinozoans in the overlying Taravale Formation (Teichert & Talent 1958; Mawson 1987; Winchester-Seeto 1996).

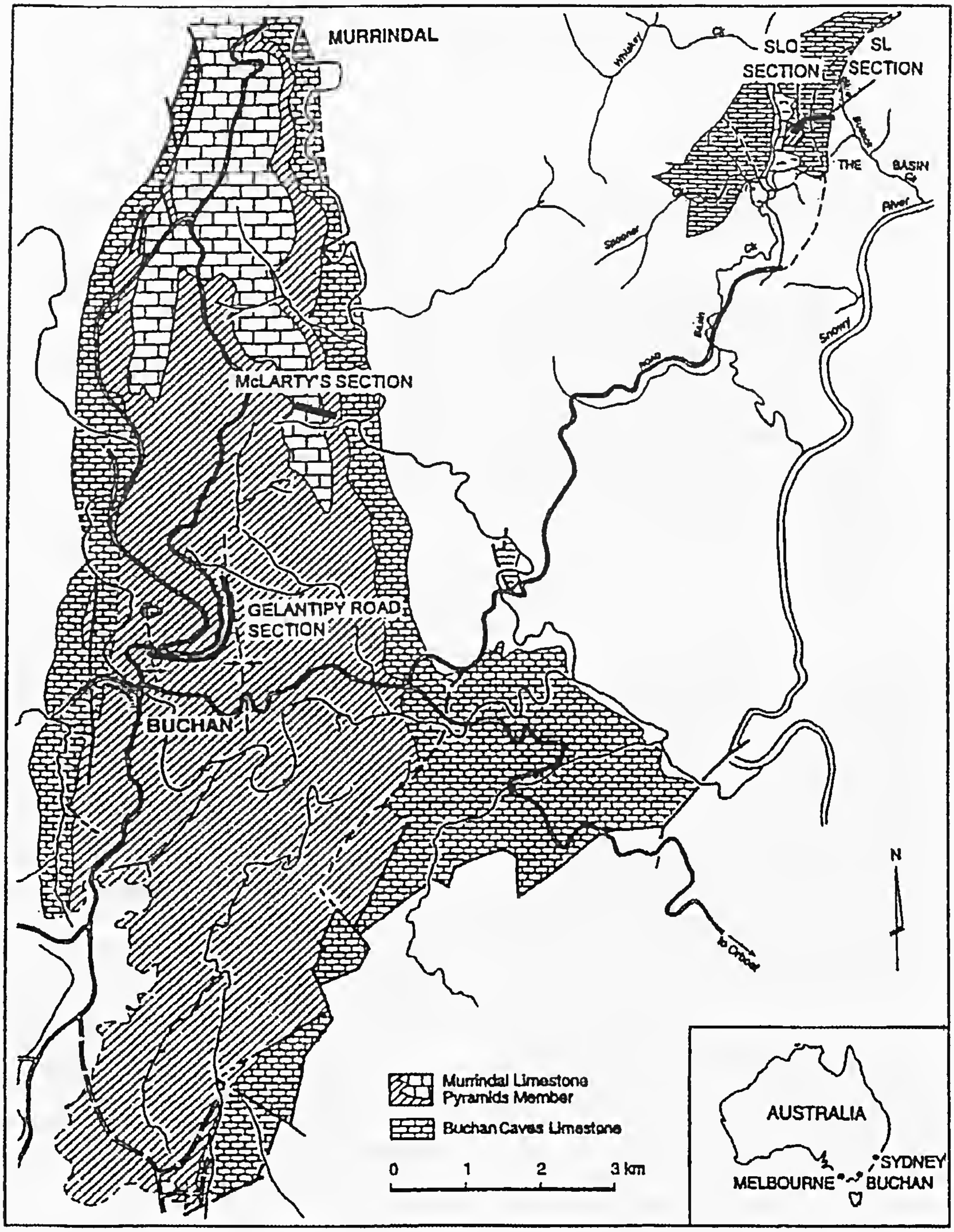


Fig. 1. Geology of Buchan Group around Buchan and The Basin, eastern Victoria (modified from Mawson et al. 1992 and Winchester-Seeto 1996).

Bed-by-bed sampling of long stratigraphic sections through the Buchan Group (Mawson 1987; Mawson et al. 1988, 1992) has resulted in acetic acid-insoluble residues containing both conodonts and microvertebrates. Identifiable microvertebrate remains occurred in three sections (Slocombe's - SL/SLO, 42 samples; McLarty's – Mc, 120 samples; and Gelantipy Road - G.Rd, 80 samples), spanning the *dehiscens, perbonus* and *inversus* zones. The turiniid thelodont scales from these sections, referred to *Turinia* sp. cf. *T. australiensis*, have been published elsewhere (Basden 1999a). This paper describes and figures the remaining microvertebrate taxa. The present study has increased the known geographic ranges of acanthodians *"Nostolepis" guangxiensis, Cheiracanthoides* sp. cf. *C. wangi* and *Rhadinacanthus*, chondrichthyan *Ohiolepis* sp., and osteichthyan *Ligulalepis toombsi*, all of which are reported for the first time from Buchan.

In the systematic descriptions below, the following abbreviations are used for measured stratigraphic sections: **SL/SLO:** Slocombe's section at The Basin, near Buchan, Buchan Caves Limestone and Taravale Formation, *?pireneae-dehiscens-perbonus* zones; **Mc:** McLarty's section near Buchan, Pyramids Member of Taravale Formation and Murrindal Limestone, *?dehiscens-perbonus* zones; **G.Rd:** Gelantipy Road section at Buchan, Taravale Formation, *perbonus-inversus* zones (See Fig. 1).

Samples are identified by the section prefix followed by the true height in metres above base of section (indicated by "m"). This is to distinguish between the true height above base of section, used in this study, and the sample number given by Mawson (1987), Mawson & Talent (1994), and Mawson et al. (1988, 1992) at the time of collection, which indicated measurement along the ground. Figured specimens are held in the palaeontology collections of the Australian Museum, Sydney, and bear the prefix AMF.

SYSTEMATIC PALAEONTOLOGY

Superclass **Gnathostomata** Gegenbauer 1874
Class **Placodermi** M'Coy 1848
Order **Acanthothoraci** Stensiö 1944
Family **Weejasperaspididae** White 1978
Genus **Murrindalaspis** Long 1984

Diagnosis (Long 1984a; Long & Young 1988). Dermal ornament of short crenulate ridges, approximately one-third as long as broad, and zones of stout polygonal or stellate tubercles. Body scales rhombic with anterior overlap flanges; exposed area with similar ornament to dermal bones.

Murrindalaspis sp.
Fig. 2A

Material. AMF101198 from Mc41.5-42.7m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), plus seven other scales and fragments from Mc3.4-3.6m, 8.5m, 18.6-21.3m, 27.7-30.5m, 41.5-42.7m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), and Mc156.1m, 180.1m (Murrindal Limestone, *perbonus* Zone).

Remarks. Long (1984a) erected the genus from medial dorsal plates recovered from the Murrindal Limestone (*perbonus* Zone) near Buchan, Victoria. The only other described specimens from southeastern Australia are a sclerotic capsule and associated plates and body scales from the *Receptaculites* Limestone near Taemas (Long & Young 1988:74, figs 9, 10) and three body scales from the same sample (Burrow & Turner 1998:687, figs 10A-E), and a preliminary report of similar scales or plate fragments from the Lochkovian-Pragian Garra Limestone in central NSW, the Murrindal Limestone, and the upper Cavan Formation (*dehiscens* Zone) at Taemas (Basden et al. 2000, fig. 7.1).

Description and Discussion. The scale crowns and plate fragments are ornamented with elongate or stellate tubercles with radiating ridges that appear nodular under high magnification. Long & Young (1988) described the elongate tubercles on the plates as being 3 to 7 times as long as wide, and Burrow & Turner (1998) specified 4-20 nodose radiating ridges on each tubercle.

The scales are generally rhombic or subcircular, with diameter 1-2mm, and a thin margin that can be either faintly radially grooved or granular-textured. Neighbouring scales overlap this thin basal margin (Long & Young 1988), which can extend all around the scale, or be confined to the anterior and lateral margins. The base varies from deeply concave with openings into the tubercles, to gently concave with no canal openings, to flat. Tubercle length varies, with central elongate tubercles, aligned antero-posteriorly, surrounded by 3-12 smaller or more circular tubercles. Commonly, anteriormost tubercles tend to be lower and rounded, and those at the posterior flatter and blade-like.

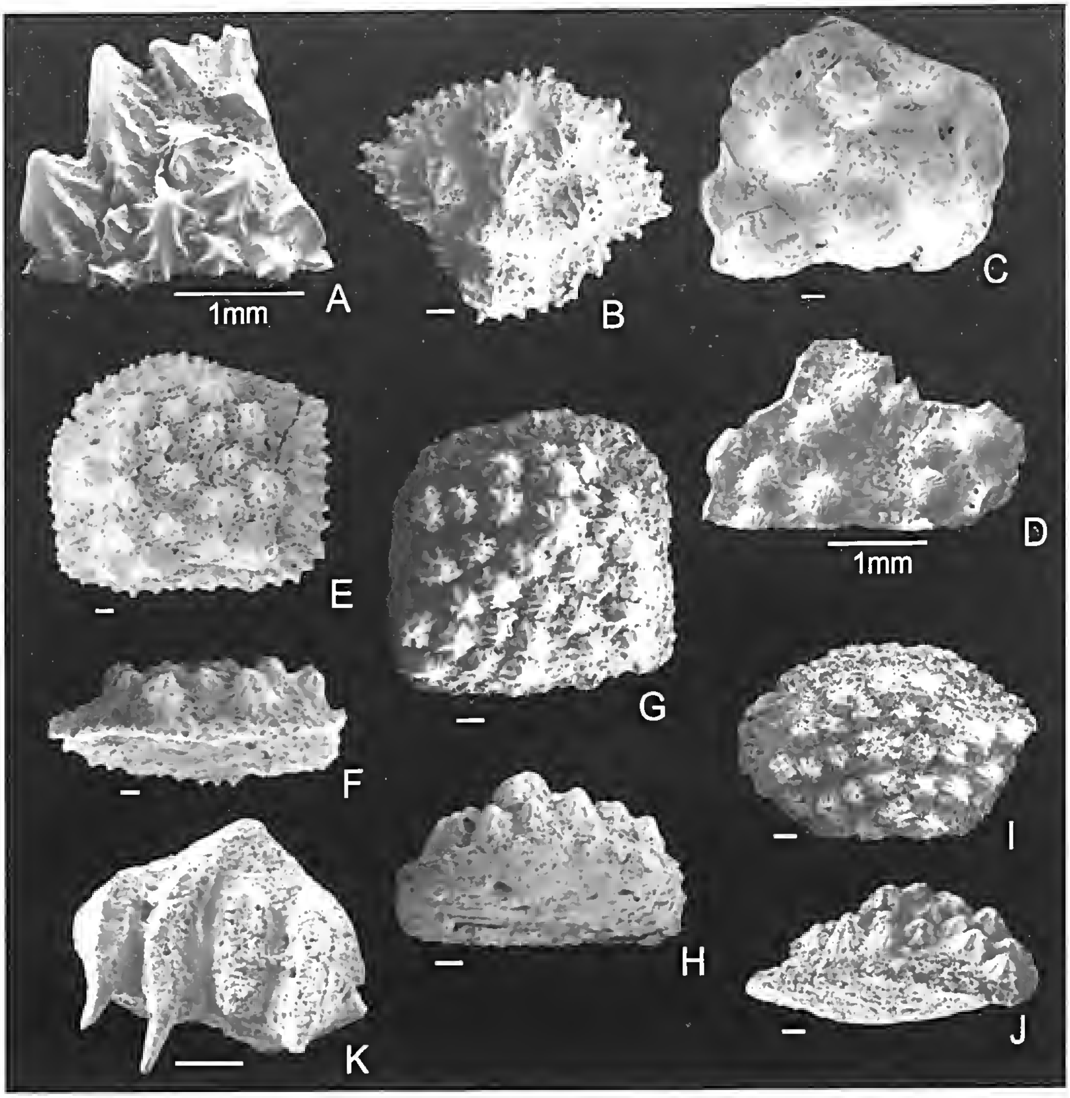


Fig. 2. Placoderm and chondrichthyan microremains from the Buchan Group. Scale bar = 100μm unless indicated otherwise. A, *Murrindalaspis* sp. Fragment AMF101198 from Mc41.5-42.7m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. B-D, *Buchanosteus* sp. B, Scale AMF101199 from SLO51-68m, Taravale Formation, *perbonus* Zone, crown view. C, Fragment AMF112353 from Mc41.5-42.7m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. D, Fragment AMF101197 from G.Rd340.5m, Taravale Formation, *inversus* Zone. E-J, *Goodradigbeeon australianum* E, F, Scale AMF112355 from SLO213m, Taravale Formation, *perbonus* Zone. E, crown view, F, lateral view. G, H, Scale AMF101196 from SL46.5m, Buchan Caves Limestone, *dehiscens* Zone. G, crown view, H, laterobasal view. I, J, Scale AMF112356 from SL46.5m, Buchan Caves Limestone, *dehiscens* Zone. I, lateral view, J, crown view. K, *Ohiolepis* sp. Scale AMF101180 from Mc91.4-93m, Murrindal Limestone, *perbonus* Zone, crown view. Some of these specimens were illustrated by Basden et al. (2000): A, fig. 10.3; B, fig. 10.4; D, fig. 10.2; G, fig. 10.1; K, fig 8.9.

Burrow & Turner (1988:687, figs 10B, C) described and illustrated histological features of *Murrindalaspis wallacei* scales.

Order **Arthrodira** Woodward 1891
Suborder **Brachythoraci** Gross 1932
Family **Buchanosteidae** White 1952

Genus **Buchanosteus** Stensiö 1945
Buchanosteus sp.
Fig. 2B-D

Material. AMF101199 from SLO51-68m (Taravale Formation, *perbonus* Zone), AMF112353 from Mc41.5-42.7m (Pyramids Member of Taravale

Formation, *dehiscens* or *perbonus* zone), AMF101197 from G.Rd340.5m (Taravale Formation, *inversus* Zone), plus 98 other scales and fragments from SL 39m, 40.8m, 42m (Buchan Caves Limestone, *pireneae or dehiscens* Zone), SL 46.5m, 49.7m, 54m, 56.2m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO 17m, 34m, 51m (Taravale Formation, *dehiscens* Zone), SLO 64m, 51-68m, 213m and G.Rd 51.2m, 51.7m, 52.5m (Taravale Formation, *perbonus* Zone), Mc 4.9-6.2m, 6.5-7.6m, 11-12.2m, 12.5-137m, 14-15.2m, 15.5-18.3m, 17.7m, 18.6-21.3m, 21.6-24.4m, 27.7-30.5m, 35.4-36.6m, 38.4-39.9m, 41.5-42.7m (Pyramids Member of Taravale Formation, *dehiscens or perbonus* Zone), Mc 88.7m, 91.4-93m, 144.8-146.3m, 156.1m, 161.5m, 189.9m, 192.5m (Murrindal Limestone, *perbonus* Zone), and G.Rd 340.5m, 343.5m (Taravale Formation, *inversus* Zone).

Remarks. The genus has undergone a series of name changes since the holotype was collected near Buchan early last century (Young 1979; Long 1984a, 1995): Chapman (1916) described the specimen as a new species of *Phlyctaenaspis*, it was reassigned by Hills (1936) to *Coccosteus*, and then by Stensiö (1945) to the new genus *Buchanosteus*. White (1952) gave Stensiö's genus a formal diagnosis, and described a similar skull fragment from Burrinjuck as *B. murrumbidgeensis*. White & Toombs (1972) subsequently referred the Burrinjuck material to a new genus, *Parabuchanosteus*. Following study of new specimens from Burrinjuck and re-examination of Chapman's type material, Young (1979) concluded that only one species, *Buchanosteus confertituberculatus* (Chapman), was represented.

In early reports, placoderm scales from Burrinjuck (Ørvig 1969; Giffin 1980) were identified as *Ohioaspis* because of their resemblance to the North American type material of *Ohioaspis tumulosus* Wells 1944. Turner & Murphy (1988) distinguished between *Ohioaspis* scales and similar scales from Nevada, Australia (Burrinjuck) and south China that they called 'buchanosteid-type', because of differences in tubercle morphology.

Burrow & Turner (1998:678-687, figs 2, 3, 4A, B, 5A-J, 6, 9C-G)) assigned scales from the McLarty member of the Murrindal Limestone, collected with dermal plates of *B. confertituberculatus* near Buchan (Long 1991), to the same species as the plates. However, Young et al. (2001) have recently reinterpreted the specimen assigned by Long to *Buchanosteus* as a primitive coccosteid rather than a buchanosteid. Burrow & Turner (1998) recognised slight morphological and histological differences from the Buchan material in two types of similar scales from Burrinjuck, which were described as Buchanosteidae indet., with tubercles on the crown either rounded and discrete or stellate and tightly-packed. Scales with stellate tubercles, from Longmenshan section, Sichuan Province, China (*dehiscens/perbonus* zones), with similar histology to buchanosteid scales from Burrinjuck, have been described as Buchanosteidae? indet.; it is likely that several primitive placoderm groups possessed scales with stellate tubercles (Burrow et al. 2000). Plate fragments and both types of scales described below resemble microremains of *Buchanosteus confertituberculatus* held in the Australian National University Collections (e.g. sample CPC16965 from an unknown locality near Taemas).

Description. Thin, subcircular or subelliptical scales, from 0.7mm diameter to 1.8mm long. Three to 20 tubercles per scale are either discrete and rounded or closely-packed and stellate. Radiating ridges sometimes extend to the tip of the tubercle (Fig. 2B). In some scales the tubercles extend to the margin, although most scales have a thin margin with radiating mucus grooves, producing a denticulate outline (Fig. 2B). The base is gently convex, flat, or gently concave, often with a few small canal openings scattered irregularly over the surface.

Plate fragments (Fig. 2C, D) are ornamented with discrete, rounded, often widely-spaced tubercles, with ridges that can radiate from a rounded top or be subparallel (e.g. some tubercles on AMF101197, Fig. 2B). The bone between the tubercles bears canal openings, especially around the base of the tubercles.

Burrow & Turner (1998, figs 3, 4A, B, 6F, G) illustrated histological features of buchanosteid indet and *Buchanosteus confertituberculatus* scales.

Genus **Goodradigbeeon** White 1978

Goodradigbeeon australianum White 1978

Fig. 2E-J

Goodradigbeeon australianum White 1978: 175, pl. 6d-f.

Goodradigbeeon australianum – Burrow & Turner 1998: 678-80, figs 7, 8A-D.

Goodradigbeeon sp. – Basden et al. 2000: 215, 217, figs 10.1, 11.4.

Material. AMF101196 and AMF112356 from SL46.5m (Buchan Caves Limestone, *dehiscens* Zone),

AMF112355 from SLO213m (Taravale Formation, *perbonus* Zone) and 30 other scales from SL39m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL 46.5m, 48.7m, 56.2m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m (Taravale Formation, *dehiscens* Zone), SLO213m and GRd51.2m (Taravale Formation, *perbonus* Zone).

Diagnosis. Description of ornament by White (1978): Ornamentation ... is tubercular, the tubercles being of the usual lemon-squeezer type with a relatively small enamel cap. When fresh the vertical ridges are seen to be pustular, the pustules at the apex forming a rosette around the cap, and the ridges of the basal intertubercular network are noticeably sharp ... There is no very marked variation in size or shape of the tubercles ...The distribution of the tubercles is close and even ... The scales are covered with minute editions of the tubercles of the general ornament, but there is usually a smooth margin around the surface. Revised description (Burrow & Turner 1998): Scales have between seven and 21 crown tubercles (average 12); the tubercles are from 0.01 to 0.02 mm wide, and bear from seven to ten radial ridges, which often branch at or near the base. The tubercles are separate, with no over-growth evident. Unlike other scales from placoderms, these have small, centrally-positioned tubercles surrounded by larger tubercles. Only rare scales have (weakly developed) mucus grooves peripherally; width of the tubercle-free crown margin varies from negligible, to about one-third of the scale width.

Remarks. White (1978) erected the taxon based on macro and microremains collected at localities near Taemas and Wee Jasper in southern New South Wales. Burrow & Turner's (1998) examination of scales from the residue of the holotype held in the collection of the Natural History Museum, London, resulted in an expanded description of the scales, and explanation of the histological differences between scales of this genus and those of *Buchanosteus*.

Description. Biconvex scales are subcircular, diamond-shaped or polygonal shaped, with the crown ornamented with 19-34 closely-spaced stellate tubercles. Central tubercles are often smaller. Between seven and ten radiating ridges on tubercles can branch near the base. A tubercle-free zone on the crown margin varies in width from negligible to approximately one-eighth the width of the scale (Fig. 2G). The base has up to three pore openings (Fig. 2H).

Burrow & Turner (1998, figs 4C, 8E) illustrated the histology of *Goodradigbeeon australianum* scales.

Class **Chondrichthyes** Huxley 1880
Subclass **Elasmobranchii** Bonaparte 1838
Order incertae sedis
Ohiolepis Wells 1944

Diagnosis (Wells 1944). Small to relatively large shagreen denticles, rounded rhombic, quadrangular, or irregularly elongate or transversely oval in outline, consisting of a broad crown ornamented by numerous spinelike tubercles with enamelled anteriorly indented, anteriorly sloping faces and acute, posteriorly inclined tips, resting directly on an often internally convex, lamellar base....anterior sides or edges of denticles devoid of tubercles over a narrow strip where overlapped by preceding denticle.

Ohiolepis sp.
Fig. 2K

Material. AMF101180 from Mc91.4-93m (Murrindal Limestone, *perbonus* Zone), plus three other scales from Mc18.6-21.3m, 35.4-36.6m (Pyramids Member of Taravale Formation, *dehiscens or perbonus* Zone), and Mc 91.4-93m (Murrindal Limestone, *perbonus* Zone).

Remarks. The genus, established by Wells (1944) from material from USA, has been reported from Australia (Schultze 1968; Giffin 1980; Turner 1982, 1993; Pickett et al. 1985; Young 1993; De Pomeroy 1994; Burrow 1997), China (Wang 1984; Zhu 2000; Zhu et al. 2000) and Germany (Ørvig 1969; Friman 1983; Vieth-Schreiner 1983). De Pomeroy (1994) discussed the differences between some of these reported occurrences, in particular the morphology and spacing of the spines on the crown, and the shape and structure of the base.

Description. Diamond-shaped scales are 0.5-1.2mm long and 0.5-0.9mm wide. The crown is fairly flat and bears 4-22 closely-packed, conical spines with rounded or pointed tips, that can either cover the crown or leave a smooth, unornamented anterior or anterolateral margin. The anterior face of the spines can be flattened or bear a longitudinal groove that is more developed on the spines with a pointed tip. The groove can extend for about half the length of the spine or almost to the

tip, with spines on the same scale showing variety of groove length. The grooved, pointed spines tend to be more steeply inclined than the smoother, round-tipped spines.

The diamond-shaped base is generally very slightly convex and centrally vaulted. On some specimens, the lateral corners of the base curve down slightly, while on others the base is gently concave with a thin marginal rim. The neck, when present, is shallow and not indented.

Class **Acanthodii** Owen 1846
Order **Climatiiformes** Berg 1940
Family **Climatiidae** Berg 1940
Genus **Nostolepis** Pander 1856
"Nostolepis" guangxiensis Wang 1992
Fig. 3A-D

Gomphonchus guangxiensis (Wang) – Turner et al. 1995: 383.
Gomphonchus? Guangxiensis (Wang 1992) – Burrow 1997: 64-66, pl. 1 figs 4-8, pl. 4 figs 1-6.
"Nostolepis" guangxiensis Wang 1992 – Burrow et al. 2000: 398-399, pl. 5.4-5.8.
?acanthodian E – Basden et al. 2000: fig. 9.13.
?acanthodian H – Basden et al. 2000: fig. 12.3.
"Nostolepis" guangxiensis Wang 1992 – Burrow 2002: 91-95, figs 4E-J, 5J-M, 12A, C, D.

Material. AMF101193 from Me41.5m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), AMF101190 from Me148.1m (Murrindal Limestone, *perbonus* Zone), plus 36 other specimens from SL46.5m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m, 34m (Taravale Formation, *dehiscens* Zone), SLO179m and G.Rd51.2m (Taravale Formation, *perbonus* Zone), Me7.9m, 15.5m, 21.6m, 27.7m, 38.4m, 41.5m (Pyramids Member of Taravale Formation, *dehiscens or perbonus* Zone), Me148.1m, 155.4m, 156.1m (Murrindal Limestone, *perbonus* Zone), and G.Rd340.5m (Taravale Formation, *inversus* Zone).

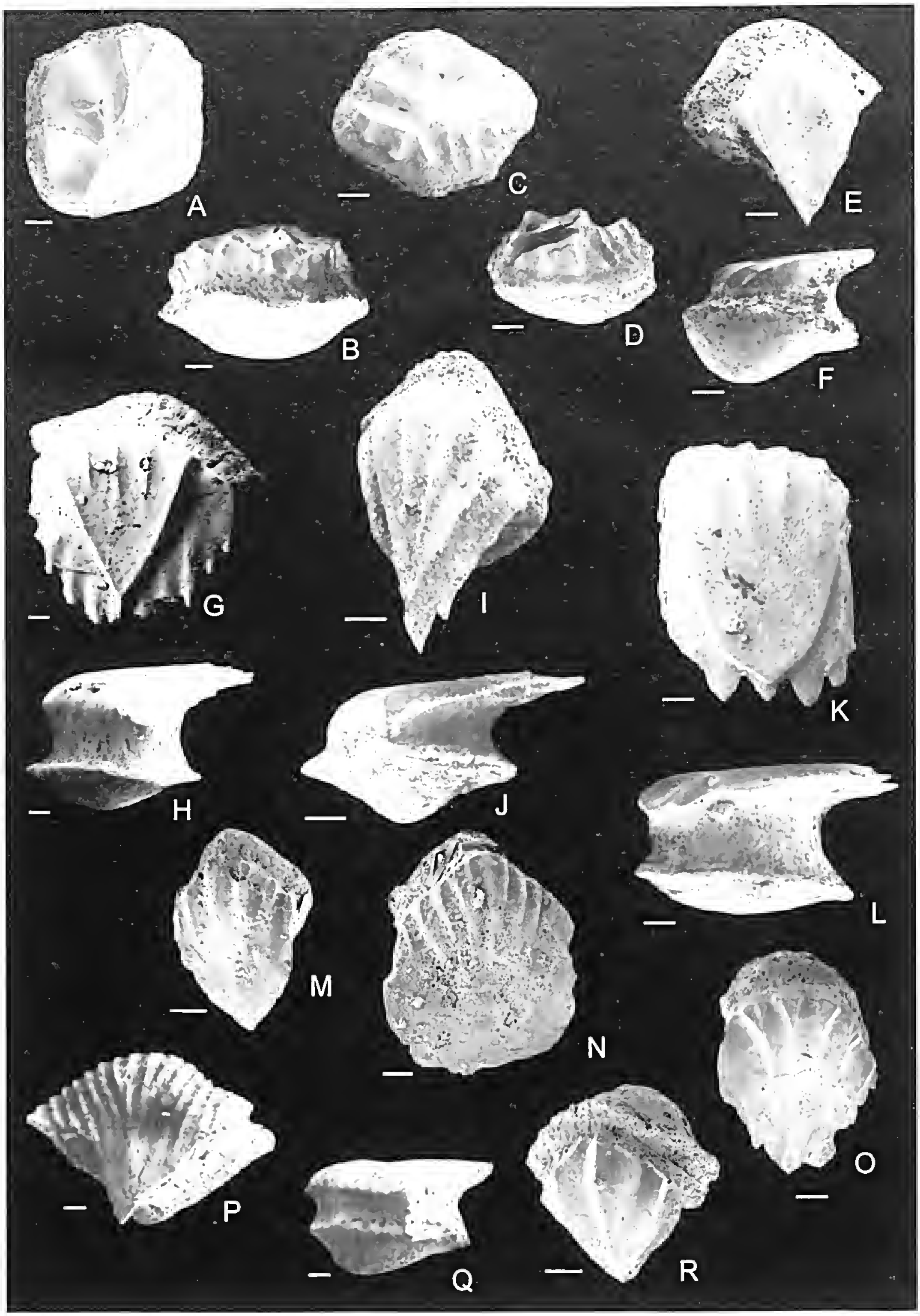
Diagnosis (Wang 1992; emended by Burrow et al. 2000). Crown flat and rhombic, with strongly developed side ridges converging posteriorly and delineating the upper crown which bears ridges on the anterior part. Sharp ridges also lead forward from the posterior point of the crown, ornamenting the dentinous region of the upper neck/lateral crown. The crown is formed of mesodentine comprising rare cell spaces and a network of dentine tubules with a well-developed system of fine, vascular canals; only very rare scales have 'Stranggewebe', and then only in the lower crown. The scale crown is smaller than the base, and the scale neck is low, clearly marked off from the base. Base is convex, with a rhombic outline, bone-cell lacunae, and radiating Sharpey's fibres.

Remarks. This taxon was erected by Wang (1992) for scales from the Ertang Formation of central Guangxi, southern China (*perbonus* Zone), based partly on his interpretation of mesodentine and Stranggewebe in the crown. Burrow (1997) noted the resemblance of similar scales from several central western New South Wales localities (Trundle Group, *kindlei-dehiscens* zones) to scales from Arctic Canada, assigned by Vieth (1980) to *Gomphonchus* sp. Cf. *G. hoppei*. She also noted that Wang's (1992) description included plates showing histological features more typical of *Gomphonchus* than *Nostolepis*: dentine tubules extending into the base, a small embryonic growth zone, numerous thin growth zones in the crown, and absence of Stranggewebe in the crown. On these grounds Burrow (1997) tentatively reassigned the species to "*Gomphonchus*?", and a preliminary report on similar scales from Longmenshan, Sichuan Province, China (*dehiscens-perbonus* zones; Turner *et al.* 1995) followed this designation.

Meanwhile, Valiukevicius (1994) had reassigned Vieth's (1980) *Gomphonchus* sp. cf. *G. hoppei* scales to a new species, *Nostolepis laticristata*, a form lacking the Stranggewebe and wide vascular canals in the crown that are usually present in *Nostolepis*. Further examination of the specimens assigned to *G.? guangxiensis* specimens from NSW revealed one scale has Stranggewebe, and another has wide vascular canals, thus leading Burrow (in Burrow et al. 2000 and Basden et al. 2000) to revert tentatively to the original nomenclature for the taxon, *"Nostolepis" guangxiensis*.

In addition to the scales from China and New South Wales mentioned above, the taxon has been reported from the Point Hibbs Formation, Tasmania (*sulcatus* Zone; Burrow et al. 1998).

Description. Morphology. Scales are small, 0.5-0.7mm, usually of similar width and length. The subrhombic crown is smaller than the base (Fig. 3A, C) and either horizontal or sloping upwards towards the posterior. The main diamond-shaped section of the crown is defined by two ridges converging at a posterior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point, and bears up to three or four anterior ribs that sometimes bifurcate at the anterior margin and generally extend almost to the posterior point of the crown. The posterolateral margins of the crown are ornamented by vertical ribs that may also bifurcate near the margin with the neck. The neck is generally shallow and of similar depth anteriorly and posteriorly (Fig. 3B). The neck-base margin is distinctly marked by a thin rim. The moderately to deeply convex base is centrally vaulted.

Histology. The base, a low-angled cone, contains bone cell lacunae and radiating Sharpey's fibre bundles. Growth zones are clearly visible in both base and crown. The crown contains Stranggewebe and a network of fine branching dentine tubules.

cf. **Nostolepis** sp.
Fig. 3E, F

Material. AMF101192 from SLO34m (Taravale Formation, *dehiscens* Zone), plus 13 other specimens from G.Rd52.5m (Taravale Formation, *perbonus* Zone), and Me3m, 4.9m, 6.5m, 7.9m, 14m, 27.7m, 33.8m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone).

Remarks. See Denison (1979) for diagnosis and De Pomeroy (1996) for comments on the distribution of this cosmopolitan genus. Nostolepid scales have been recorded from the Early Devonian of eastern Australia in the Broken River Group (*serotinus* Zone) and Martins Well Limestone (*pesavis-sulcatus* zones) in Queensland (Turner 1991, 1993; De Pomeroy 1996; Turner et al. 2000), and the Condobolin Formation, Garra and Windellama limestones, Trundle and Yarra Yarra Creek groups in New South Wales, in horizons dated from Lochkovian to early Emsian (Turner 1991, 1993; Burrow 1997; Basden et al 2000).

Description. Small scales 0.4-0.7mm long and wide. The subtriangular crown slopes up from a rounded anterior margin to a pointed posterior that extends beyond the base (Fig. 3E). Short, low, parallel ridges ornament the anterior part of the crown. The neck is shallow anteriorly and deeper and concave posteriorly (Fig. 3F), with no or few visible pore canal openings. The base and neck are separated by a distinct rim (Fig. 3F). The centrally convex base is subrhombic, with anterior and posterior corners slightly rounded and lateral corners more pointed (Fig. 3E). Faint concentric lines visible on the base possibly represent different growth zones.

Genus **Nostolepoides** Burrow 1997
Nostolepoides platymarginata Burrow 1997
Fig. 3G-L

nostolepid scale – Philip 1965, pl. 8.38. – Turner 1991: pl. 3B.
acanthodian scale – Turner 1991: pl. 5H.
Nostolepoides platymarginata Burrow 1997: 45-57, pl. 1 figs 1-3, pl. 2 figs 7-10,12.
Nostolepoides platymarginata Burrow 1997 – Basden 1999b: 535, pl. 2 figs 2-3.
Nostolepoides platymarginata Burrow 1997 – Burrow 2002: 83-87, figs 5D-I, 8A-K.

Material. AMF101183 from SLO8.5m, AMF112378 from SLO51m (Taravale Formation, *dehiscens* Zone), AMF101185 from SLOc85m (Taravale Formation, *perbonus* Zone), plus 396 specimens from SL39m, 39.7m, 40.8m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL 46m, 48.7m, 58.55m, (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m, 17m, 34m, 44m, 51m (Taravale Formation, *dehiscens* Zone), SLO55m, 64m, 68m, 72m, 85m, 170m, 179m, 213m and G.Rd 51.2m, 52.5m (Taravale Formation, *perbonus* Zone), Me3.4m, 4.9m, 7.9m, 11m, 15.5m, 18.6m, 21.6m, 24.2m, 27.7m, 30.8m, 36.9m, 41.5m,

Fig. 3. Acanthodian microremains from the Buchan Group. Scale bar = 100µm. A-D, "*Nostolepis*" *guangxiensis*. A, B, Scale AMF101193 from Me41.5-42.7m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. A, crown view, B, lateral view. C, D, Scale AMF101190 from Me148.1-149.4m, Murrindal Limestone, *perbonus* Zone. C, crown view, D, lateral view. E, F, cf. *Nostolepis* sp. Scale AMF101192 from SLO34m, Taravale Formation, *dehiscens* Zone. E, crown view, F, lateral view. G-L, *Nostolepoides platymarginata* G, H, Scale AMF101183 from SLO8.5m, Taravale Formation, *dehiscens* Zone. G, crown view, H, lateral view. I, J, Scale AMF112378 from SLO51m, Taravale Formation, *dehiscens* Zone. I, crown view, J, lateral view. K, L, Scale AMF101185 from SLO85m, Taravale Formation, *perbonus* Zone. K, crown view, L, lateral view. M, *Cheiracanthoides* sp. cf. *C. comptus*. Scale AMF101215 from Me88.7m, Murrindal Limestone, *perbonus* Zone, crown view. N, O, *Cheiracanthoides* sp. cf. *C. wangi* N. Scale AMF101214 from SLO213m, Taravale Formation, *perbonus* Zone, crown view, O, Scale AMF101216 from Me160.6m, Murrindal Limestone, *perbonus* Zone, crown view. P, Q, *Rhadinacanthus*? sp. Scale AMF101189 from SL46.5m, Buchan Caves Limestone, *dehiscens* Zone. P, crown view, Q, lateral view. R, *Gomphonchus bogongensis* Scale AMF101217 from SLO17m, Taravale Formation, *dehiscens* Zone, crown view. Some of these specimens were illustrated by Basden et al. (2000): A, fig. 9.11; C, fig.9.8; E, fig. 9.10; G, fig. 9.1; K, fig. 9.3; P, fig. 9.7.

43m (Pyramids Member of Taravale Formation, *dehiscnes* or *perbonus* Zone), Me88.7m, 91.4m, 150.9m, 154m, 155.4m, 156.1m, 156.4m, 160m, 160.6m, 163.8m, 180.1m, 182.9m, 189.9m, 190.5m, 192.5m, 227.4m (Murrindal Limestone, *perbonus* Zone), G.Rd 340.5m (Taravale Formation, *inversus* Zone).

Diagnosis (Burrow 1997). Scales range from 0.15 to 1.0mm wide. They have a bi-level crown; the upper crown is delineated by ridges converging in the posterior half of the crown and with subparallel ribs between them. The lower crown is a latero-posterior, overhanging ledge of varying width and outline. The neck is high and concave (morphotype 1) or low anteriorly (morphotype 2), and the base is moderately vaulted. The crown is composed of mesodentine. Large bone cell lacunae and their processes interconnect throughout the base.

Remarks. These Victorian scales resemble Morphotype 1 scales described by Burrow (1997) from the Gleninga (*pireneae-dehiscens* zones) and Troffs formations (*kindlei-dehiscens* zones) in central NSW. They are morphologically similar to the Late Silurian-Early Devonian *Nostolepis striata* Pander but can be distinguished from that species histologically and by the posterolateral ledge of the crown being wide and/or irregular and continuing around the posterior point, as discussed by Burrow (1997). One of the scales figured by Philip (1965, pl. 8.38) from the Tyers area has been assigned by Burrow (1997) to *Nostolepoides platymarginata*.

Description. Morphology. Scales range in width from 0.5 to 1.2mm. The subrhombic crown consist of two levels. The higher central triangular section is enclosed by two strong radial ridges extending from the anterior margin and converging in a posterior point (Fig. 3G, I), with 3-5 short anterior subparallel ribs that extend up to halfway towards the posterior point, and can bifurcate at the anterior margin (Fig. 3I). The lower level of the crown is a thin posterolateral platform of varying width, that extends beyond the posterior point of the upper crown and can have an irregular (Fig. 3I) or even denticulate margin (Fig. 3G, K). The fairly deep neck is clearly defined, concave, and deeper posteriorly. Some scales have a row of up to ten pore canal openings on the anterior neck (Fig. 3H). The subrhombic base is gently convex, centrally vaulted and separated from the neck by a distinct rim (Fig. 3H, J, L).

Histology. Thin sections show a clear demarcation between crown and base, with a large initial (embryonic) growth zone. Both base and crown have distinct growth zones. The base contains bone cell laeunae and radiating bundles of Sharpey's fibres. The branching dentine tubules in the crown are confined to individual growth zones and are less apparent in outermost zone(s).

Genus **Cheiracanthoides** Wells 1944
Cheiracanthoides sp. cf. **C. comptus**
Fig. 3M

Material. AMF101215 from Me88.7m (Murrindal Limestone, *perbonus* Zone), and 93 other scales from SL39m, 40.8m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL46.5m, 58.6m (Buchan Caves Limestone, *dehiscens* Zone), SLO 8.5m, 17m, 34m, 51m (Taravale Formation, *dehiscens* Zone), SLO 55m, 64m, 72m, 85m, 213m and G.Rd50.9m, 52.8m (Taravale Formation, *perbonus* Zone), Me 15.5m, 33.8m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Me88.7m, 156.1m, 160.6m, 189.9m, 190.5m (Murrindal Limestone, *perbonus* Zone), G.Rd339.7m (Taravale Formation, *inversus* Zone).

Remarks. The cosmopolitan species *Cheiracanthoides comptus* is frequently reported from Early and Middle Devonian horizons (e.g. Wells 1944; Gross 1973; Denison 1979; Valiukevicius 1979, 1985, 1994, 1998; Vieth 1980; Vieth-Schreiner 1983; Poltnig 1984; Boucot et al. 1989; Turner 1991, 1993; Wang 1992; De Pomeroy 1995, 1996; Basden et al. 2000; Burrow et al. 2000; Zhu 2000; Zhu et al. 2000). Scales from the *Receptaculites* Limestone at Burrinjuck have been assigned to the genus (Giffin 1980, fig. 5), but it is possible that *C. comptus* has become a "bucket" taxon comprising several different form species or even genera with a similar morphology; see De Pomeroy (1996) for discussion.

Recent work has resulted in the erection of several new species (Valiukevicius 1998, Burrow et al. 2000). The diagnosis and description, originally established by Wells (1944), have been refined so that more subtle differences in morphology and histology can be attributed to different species. For example, from material from the East Baltic and Byelorussia, Valiukevicius (1998) has proposed three new species – *Cheiracanthoides planus* (smaller than *C. comptus*, with fewer ridges on the crown and absence of the

narrow unsculptured rim around the crown anterior), *C. nativus* (lacking the smooth lateral areas on the crown of *C. comptus*) and *C. estonicus* (scales from the Eastern Baltic previously assigned to *C. comptus*). Burrow et al. (2000), studying residues from Sichuan Province, China, have distinguished *C. dolosus*, with a bevelled anterior crown rim, short regularly-spaced ridges, and Stranggewebe extending into the anterior crown, and *C. wangi* (discussed below).

Description. The elliptical or subrhombic crown is flat, slightly wider than long, and ornamented on the anterior third to half by between four and ten radiating or subparallel low rounded ridges separated by broad furrows. The indented neck is a consistent depth from anterior to posterior. The crown extends beyond the base posteriorly. The base is diamond-shaped, moderately convex and and centrally vaulted, with the neck-base margin marked by a thickened rim.

Cheiracanthoides wangi Burrow et al. 2000
Cheiracanthoides sp. cf. **C. wangi**
Fig. 3N, O

Material. AMF101214 from SLO213m (Taravale Formation, *perbonus* Zone), AMF101216 from Mc160.6m, and two scales from Mc88.7m, 160.6m (Murrindal Limestone, *perbonus* Zone).

Diagnosis. Scales with a fairly flat crown, which is more than twice as long as wide, and with anterior edges often forming a sharp angle. The anterior crown is ornamented with between three and ten sharp, strongly-developed, sub-convergent ridges which extend about one-third of the crown length. The lateral areas of the anterior crown are smooth: i.e., the ridges span the medial two-thirds to three-quarters of the anterior crown. More than half of the crown overhangs the posterior limit of the base; the overhanging section is very thin. The neck is concave all round, falling away sharply from the anterior crown edge, and deepening slightly towards the posterior. The base/neck junction is a strongly marked rim; the base is moderately to strongly vaulted, and projects slightly forwards of the crown. "Stranggewebe" is only formed in the upper neck/crown area of the posterior growth zones. Bone cell lacunae are preserved in the apex of the base (Burrow et al 2000).

Remarks. The species was described by Burrow et al. (2000: 397-398, figs 2.10-2.12, pl. 3.1-3.7, 3.9-3.10) from Longmenshan, Sichuan Province, China (*dehiscens-perbonus* conodont zones), and is also reported from the late Pragian – early Emsian (?*kindlei-perbonus* zones) in the Guangxi and Sichuan provinces (Zhu 2000; Zhu *et* al. 2000). It is now considered an index fossil for the *dehiscens* Zone (Burrow 2000).

The Australian scales described here differ in some features from the Chinese specimens. The central region of the crown generally tends to have ridges closer to parallel, and with a more distinct difference between this central parallel section and the anterior section where the ridges radiate; and the length of the crown, which in some scales is greater than the width, is, even in broken specimens, generally nowhere near twice the width, as is the case with *C. wangi* scales from China. However, since all the Victorian specimens have the thin posterior section of the crown broken off, it is difficult to determine precisely the initial dimensions and length/width ratios of the scales.

Description. Morphology. Scales are approximately 0.8 to 1.2 mm wide, and 0.9 to 1.2 mm from anterior margin to broken posterior edge. The flat subcircular or subrhombic crown slopes slightly upwards towards the posterior. The anterior part of the crown bears between five and seven sharply-crested, radiating ridges that become closer together and subparallel in the central crown area. At the anterior, these ridges can extend down a short distance onto the upper part of the neck. The posterior part of the crown is unornamented, thin and commonly broken.

The neck is generally high and concave, and can become deeper posteriorly. Several small round pore canal openings are found in the central part of the anterior neck, and more elongate openings are high up under the overhanging crown on the posterior neck. The base is very deeply convex, and centrally vaulted. The base and neck are separated by a swollen rim that extends into lateral and posterior flanges.

Histology. The base inserts high into the crown. Both base and crown have distinct growth zones, those in the base parallel to the lower surface. The base contains bone cell lacunae with branching tubules and radiating Sharpey's fibre bundles. All but the outermost growth zones of the crown contain dense outwardly-directed tubules, all confined within individual growth zones.

Family **Diplacanthidae** Woodward 1891
Genus **Rhadinacanthus** Traquair 1888
Rhadinacanthus? sp.

Fig. 3P, Q

Material. AMF101189 from SL46.5m (Buchan Caves Limestone, *dehiscens* Zone) and seven specimens from SL39m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL46.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO51-68m (Taravale Formation, *perbonus* Zone), and Mc160.6m (Murrindal Limestone, *perbonus* Zone).

Remarks. The genus *Rhadinacanthus* is considered a possible synonym for *Diplacanthus* (Denison 1979; see Burrow et al. 2000, for discussion).

Description. Scales have a kite-shaped crown that is wider than long. The flat crown has a curved anterior margin and pointed lateral and posterior corners (Fig. 3P). The posterior crown overhangs the base only a short distance (Fig. 3Q). Approximately 15 closely-spaced sharp-crested anterior ribs on the crown converge slightly towards the crown centre and extend back to about mid-way.

The indented neck is clearly defined from both crown and base by a distinct rim. The neck has up to ten pore openings low on the neck close to the neck-base margin both anteriorly and posteriorly, but shows no sign of the wart-like bulges at the posterior, as described by Gross (1973) in *R. balticus*. The base is gently convex.

Order **Ischnacanthiformes** Berg 1940
Family **Ischnacanthidae** Woodward 1891
Genus **Gomphonchus** Gross 1971
Gomphonchus? bogongensis Burrow 1997
Fig. 3R

Gomphonchus? bogongensis Burrow 1997: 67-71, pl. 1 figs 9-12, 16, pl. 4 figs 8-16.
Gomphonchus? bogongensis Burrow 1997 – Burrow et al. 1998: 13, fig. 3B-C.
Gomphonchus? bogongensis Burrow 1997 – Basden 1999b: 536-8, pl. 2 figs 8-9.
Ischnacanthid indet. C – Lindley 2002: fig. 9A-I.

Material. AMF101217 from SLO17m (Taravale Formation, *dehiscens* Zone), and 152 specimens from SLO39m, 40.8m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL46.5m, 48.7m, 53.2m, 54m, 56.2m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m (Taravale Formation, *dehiscens* Zone), SLO170m, 213m, G.Rd51.7m, 52.5m (Taravale Formation, *perbonus* Zone), Mc 4.9m, 6.5m, 8.5m, 11m, 14m, 15.5m, 18.6m, 30.8m, 33.8m, 35.4m, 36.9m, 38.4m, 43m, 44.5m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Mc150.9m, 154m, 155.4m, 156.1m (Murrindal Limestone, *perbonus* Zone).

Diagnosis (Burrow 1997). Small scales, 0.15 to 0.7mm wide, with a subtriangular crown, low neck, and a moderate to large convex base. There are two main morphotypes: in morphotype 1, the crown has a curved fan shape, ornamented with sharp fan-like ridges and grooves, and slopes upwards from the anterior edge to a posterior point. Morphotype 2 scales have a crown with an upper sub-triangular, and a lower lateral, level which can be greatly elongated posteriorly. The scale crown is composed of orthodentine. All scales have a 'scalloped' antero-lateral crown edge.

Remarks. Scales resemble Morphotypes 1 and 2 described by Burrow (1997) from the Trundle Beds (now Troffs Formation) and Gleninga Formation in central NSW. Revised dating of the horizons by Sherwin (1996) now places the horizons with these scales into *pireneae-dehiscens* zones. Scales of *G.? bogongensis* are also reported from the *sulcatus* Zone at Point Hibbs (Burrow et al. 1998).

Morphotypes 1 and 2 can both be distinguished from *Nostolepoides platymaginata* scales by the scalloped anterior margin of the crown, and the increased depth of the neck towards the posterior, and Morphotype 1 also by the lack of lowered lateral crown ledges. Morphotype 1 is distinguished from *"Nostolepis" guangxiensis* by the short anterolateral ridges not continuing around below the posterior point of the crown (Burrow 1997).

Description. Morphology. Subrhombic or diamond-shaped scales have the crown and base approximately a similar shape, and the crown generally smaller than the base. Width ranges from 0.4 to 1.2mm. The fan-shaped crown has 4-8 radiating anterior ridges with sharp crests, separated by deep furrows; these ridges can be less than half the crown length, or extend virtually to the posterior point of the crown. These features in combination with the curving down of the anterior crown towards the neck give the scalloped anterior margin to the crown that is distinctive of this form.

In Morphotype 2 scales the posterior point of the crown is more elongated than in Morphotype 1, and can extend slightly beyond the base. Short anterolateral

ridges on the sides of the crown do not continue beyond the posterior point. These anterolateral ridges vary, from very short anterior ridges that give a bifurcating appearance to the marginal lateral ribs of the crown, or do not even quite meet the marginal lateral ribs, to ridges found high on the lateral margins of the crown, not extending far onto the neck.

The neck is short anteriorly, not very indented, and widens posteriorly. A row of pore canal openings on the posterior neck is better developed in some scales, with the canal openings elongated.

The base is moderately to strongly convex, centrally vaulted and separated from the neck by a distinct rim that is particularly pronounced at the lateral and posterior corners. Concentric markings parallel to the neck/base rim indicate presence of Sharpey's fibres.

Histology. Scales are generally not well preserved, with minimal histological detail revealed in many scales. However, growth zones in both base and crown are apparent. The base contains Sharpey's fibre bundles, a fine network of interconnecting tubules, and sparse bone cell lacunae. The crown contains fine branching tubules that are sparse in the outermost growth zone.

Class **Osteichthyes** Huxley 1880
Subclass **Actinopterygii** Klein 1885
Order **Palaeonisciformes** Hay 1929
Ligulalepis Schultze 1968
Ligulalepis toombsi Schultze 1968
Fig. 4A

Ligulalepis toombsi Schultze 1968: 345-351, figs 1-6, pl. 1 figs 1-8, pl. 4, fig. 1.
Ligulalepis toombsi Schultze 1968 – Giffin 1980: 10-11, fig. 10.
Ligulalepis toombsi Schultze 1968 – Burrow 1994: 177-184, figs 2-5.
Ligulalepis toombsi Schultze 1968 – Basden et al. 2000: fig. 8.7.

Material. AMF 101178 from SLO34m (Taravale Formation, *dehiscens* Zone).

Diagnosis (translated from Schultze 1968). Genus … with deep scales on the flanks; scales close to the shoulder girdle are 3-4 times deeper than long; on the anterior upper corner there is a very marked projection, which makes a sharp angle to the front edge; ventral edge slopes away from the front edge towards the back end. Strong peg and correspondingly deep socket; keel quite deep; secondary keel, on the back edge of which are openings of most canals. Development of the ganoin surface common to all species in the genus. Ganoin well-developed, partly divided into separate ribs backwards from front edge, ornamented towards front edge with small longitudinal striations which are absent in small scales; back edge comb-like; front edge slightly or strongly concave, anterior lower corner rounded, ventral edge straight.

Remarks. Schultze (1968) erected the taxon from material in residues from the 1955 and 1963 Burrinjuck expeditions by H.A. Toombs (Natural History Museum, London), from spot localities in horizons from the Cavan Formation to the Warroo Limestone. Giffin (1980) figured similar scales from the *Receptaculites* Limestone at Taemas (residues of B.D.E. Chatterton's processing of trilobites and brachiopods) as did Burrow (1994) from the Troffs and Gleninga formations of central New South Wales (*pireneae-dehiscens* zones). Other Devonian palaeoniscoid genera described from Australia are *Terenolepis turnerae* Burrow 1995 from Connemarra Formation, Trundle Group and Garra Limestone (Hocking in Basden et al 2000), *Howqualepis rostridens* from the Frasnian Avon River Group at Mt Howitt, Victoria (Long 1988, figs 32, 33), and *Mimia toombsi* and *Moythomasia durgaringa* from the Givetian-Frasnian Gneudna Formation and Frasnian Gogo Formation (Gardiner & Bartram 1977; Trinajstic 1999a, figs 3, 4; 1999b, figs 4, 5).

Description. The subrectangular scale has a free field ornamented with unfused ridges, a denticulate caudal margin and a smooth depressed field along the curved rostral edge. A rounded, tongue-shaped process projects rostro-dorsally and more pointed dorsal peg would have fitted into a corresponding socket on the ventral edge of the scale above. On the basal surface dorsoventrally oriented primary and secondary keels are separated by a groove.

Subclass **Sarcopterygii** Romer 1955
Division **Rhipidistia** Cope 1887
Order **Onychodontiformes**
Onychodontiformes gen. et sp. indet.
Fig. 4B-J

Material. Scales with U-shaped tubercles: AMF118232 from Mc7.9-9.1m (Pyramids Member

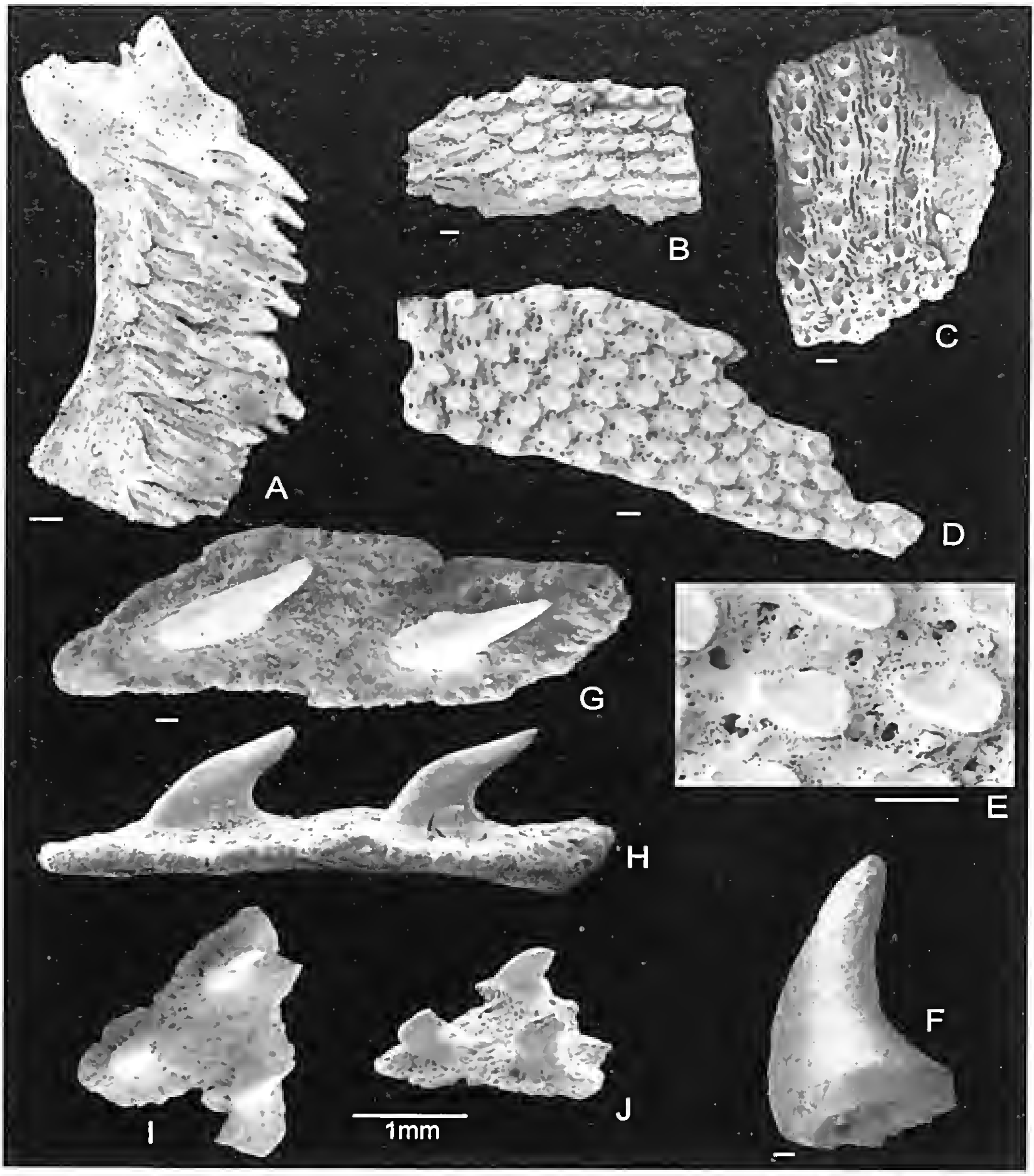

Fig. 4. Osteichthyan microremains from the Buchan Group. Scale bar = 100μm unless indicated otherwise. A, *Ligulalepis toombsi* Scale AMF101178 from SLO34m, Taravale Formation, *dehiscens* Zone. B-J, Onychodontiformes gen. et sp. indet. B, Fragment AMF118232 from Mc7.9-9.1m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone, crown view. C, Fragment AMF101181 from Mc156.1m, Murrindal Limestone, *perbonus* Zone, crown view. D, E, Fragment AMF118231 from GRd340.5m, Taravale Formation, *perbonus* Zone. D, crown view, E, detail of crown ornament. F, Tooth AMF101220 from SLO55m, Taravale Formation, *perbonus* Zone. G, H, Scale AMF101182 from Mc43-44.2m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. G, crown view, H, lateral view. I, J, Scale AMF118236 from GRd340.5m, Taravale Formation, *inversus* Zone. I, crown view, J, coronolateral view. Some of these specimens were illustrated by Basden et al. (2000): A, fig. 8.7; C, fig. 8.10; G, fig. 8.11; H, fig. 8.12.

of Taravale Formation, *dehiscens* or *perbonus* Zone), AMF101181 from Mc156.1m (Murrindal Limestone, *perbonus* Zone), AMF118231 from G.Rd340.5m (Taravale Formation, *perbonus* Zone), plus 37 other specimens from G.Rd340.5m (Taravale Formation, *perbonus* Zone), Mc3m, 7.9-9.1m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Mc151.5m (Murrindal Limestone, *perbonus* Zone).
Teeth: AMF101229 from SLO55m (Taravale formation, *perbonus* Zone), plus 157 other specimens from SLO8.5m, 17m, 34m, 44m, 51m (Taravale Formation, *dehiscens* Zone), SLO64m, 213m, G.Rd50.9m, 52.3m (Taravale Formation, *perbonus* Zone), Mc3m, 3.4-3.6m, 4.9-6.2m, 6.5-7.6m, 7.9-9.1m, 11-12.2m, 12.5-13.7m, 14-15.2m, 15.5-18.3m, 17.7m, 18.6-21.3m, 21.6-24.4m, 24.4-27.4m, 27.7-30.5m, 30.8-33.5m, 33.8-35.1m, 35.4-36.6m, 36.9-38.1m, 38.4-39.9m, 43-44.2m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Mc91.4-93m, 150.9m, 151.5m, 155.4m, 156.1m, 156.4m, 160.6m, 161.5m, 163.1m, 163.8m, 192.5m (Murrindal Limestone, *perbonus* Zone), Mc224-225.6m, 225.9-227.1m, 227.4-228.6m (Upper Taravale Formation, *perbonus* Zone), G.Rd340.5m (Taravale Formation, *inversus* Zone).

Scales with curved denticle: AMF101182 from Mc43-44.2m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), AMF118236 from G.Rd340.5m (Taravale Formation, *inversus* Zone).

Remarks. Inclined U-shaped tubercles with a central depression are found on scales of several fish groups, thus limiting their utility for identification. Dipnoan scales have been described with this type of tubercular ornament in conjunction with cosmine and Westoll lines (the primitive dipnoan *Dipnorhynchus sussmilchi* from Buchan and Taemas; Thomson & Campbell 1971), but as no cosmine is preserved on the Victorian scales, dipnoan affinity is probably precluded. Apart from dipnoans, the only other common osteichthyan remains known from the region are actinopterygians and onychodontids, and since actinopterygians are not known to have denticles, the scales and fragments described here probably belong to onychodonts.

Description. Scales with U-shaped tubercles. Figured specimens are broken fragments that exhibit a variety of morphologies of the crescent- or U-shaped tubercles. The tubercles themselves can be fairly flat with smooth, very slightly concave anterior margins (Fig. 4D), oriented in rows (Fig. 4C), or more elongate and irregularly shaped with a distinct depression in the anterior face (Fig. 4B).

The detail of specimen AMF118231 (Fig. 4E) shows the bone surface between the dentine tubercles pitted with irregular vascular canal openings, whereas in AMF101181 (Fig. 4C) the bone between the tubercles is striated by rows of elongate canal openings.

Teeth. Simple curved conical teeth up to 2mm long can be slender, tapering to a sharp point, or thicker with a rounded apex (Fig. 4F). The base of the laniary and interlaniary teeth is circular and constricted. All specimens are hollow, with the cusp in better-preserved examples covered in finely striated enamel, although preservation is not sufficient to discern micro-patterns in the enamel.

Scales with curved denticle. Articulated diamond-shaped scales (Fig. 4G) have a central curved, inclined, conical, unstriated denticle. The main part of the scale consists of flat bony tissue; in contrast, the denticles are noticeably smoother and shinier. The only ornament on the scales is a series of faint radiating grooves on the base around each denticle (Fig. 4I, J). The basal surface of the scales generally is flat and unornamented, although specimen AMF101182 (Fig. 4G, H) has faint grooves corresponding to the margins of the articulated diamond-shaped scales, and the three articulated scales in specimen AMF118236 (Fig. 4I, J) are slightly concave centrally. A broken denticle (Fig. 4I, J) shows a very narrow longitudinal canal, situated slightly off-centre towards the outer edge of the denticle.

CONCLUDING REMARKS

Acanthodian scales are the most common elements of the fauna (Fig. 3). Climatiid scales of *Nostolepoides platymarginata* and *Cheiracanthoides* sp. cf. *C. comptus* are spread throughout the three sections, and occur in all four formations (Buchan Caves and Murrindal limestones, Taravale Formation, and the Pyramids Member of the Taravale Formation). In SL/SLO section, *Gomphonchus? bogongensis* is much more common in the Buchan Caves Limestone.

The "nostolepid" scale (*sulcatus* Zone) from Tyers in Victoria, illustrated by Philip (1965) and Turner (1991, pl. 3B), is similar to some of these scales, but another similar scale was assigned by Vieth (1980, pl. 6, fig. 15) to *Cheiracanthoides comptus*. More elongate scales (e.g. Fig. 3E, F) resemble the scale from

Burrinjuck in southern New South Wales assigned to *C. comptus* by Giffin (1980, fig. 5), but these are also similar to a scale from Algeria assigned by Blieck et al. (1984, pl. 1, fig. 4) to *Nostolepis* sp. Similar crown morphologies but different shape (Fig. 3G-L) might indicate scales from different parts of the same fish, but V.T.Young (1995) recorded little shape variation in several articulated acanthodian taxa from the Early to Middle Devonian of Britain. Other scales are compared with *Cheiracanthoides wangi* (Fig. 3N, O), recently described from *dehiscens-perbonus* zones of China (Burrow et al. 2000), and *Rhadinacanthus* (Fig. 3P, Q).

Scales of arthrodires *Goodradigbeeon* and *Buchanosteus* are the most abundant placoderm microremains in the Buchan measured stratigraphic sections. Small plate fragments (Fig. 2E, F) recorded from horizons in the *dehiscens – inversus* interval have the same ornament as originally figured by White (1952, pl. 30) for *Buchanosteus murrumbidgeensis*. Other plate fragments with more elongate tubercles (Fig. 2A) are compared with *Murrindalaspis* sp. (e.g. Long & Young 1988).

Osteichthyan remains from Buchan include a scale of the actinopterygian *Ligulalepis toombsi* (Fig. 4A), and cosmine covered elements that may belong to either dipnoans or porolepiforms (see De Pomeroy, 1996: 433). Similar cosmine-covered scales described from an Early Devonian dipnoan by Barwick et al. (1997) have rows of odontodes as seen in porolepiform scales, (e.g. Fig. 4B-E; Ørvig, 1969, fig. 6). However, the scales of *Dipnorhynchus*, the only named dipnoan from Buchan, have a different morphology, with coarser rounded tubercles on the scale margins (see Thomson & Campbell 1971, figs 86-89). By the Late Devonian these tubercle zones had been lost from dipnoan scales (Pridmore & Barwick 1993). Rhombic plates, each with a central hooked denticle (Fig. 4G-J) may be small elements from inside the bucco-pharyngeal cavity of an onychodontid (P.Janvier, pers. comm.). In section SL/SLO, both osteichthyans present (*Ligulalepis toombsi* and *Onychodus* sp.) occurred only in the Taravale Formation, and were absent from the Buchan Caves Limestone.

A chondrichthyan scale similar to *Ohiolepis* sp. (Fig. 2K) is the first chondrichthyan reported from the Buchan sequence.

The first thelodont scales described from the Buchan area were part of the current study (Basden 1999a). All ten scales were recovered from horizons dated *dehiscens-perbonus* zones, and have been assigned to *Turinia* sp.cf. *T. australiensis*.

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TWO ALPINE WOLF SPIDERS OF AUSTRALIA: *ARTORIA ALTA* SP. NOV., AND THE MALE OF *LYCOSA MUSGRAVEI* MCKAY, 1974 (ARANEAE, LYCOSIDAE)

VOLKER W. FRAMENAU

Department of Zoology, University of Melbourne, Parkville, Victoria 3010
Current address: Department of Terrestrial Invertebrates, Western Australian Museum, Francis St, Perth, Western Australia 6000

FRAMENAU, V. W., 2003: 06:15. Two Alpine Wolf Spiders of Australia: *Artoria alta* sp. nov., and the male of *Lycosa musgravei* McKay, 1974 (Araneae, Lycosidae). *Proceedings of the Royal Society of Victoria* 115(1): 27-34. ISSN 0035-9211

A new wolf spider species from the alpine region of the Australian Alps, *Artoria alta* sp. nov., is described and the male of *Lycosa musgravei* McKay, 1974 is illustrated for the first time. Dense pubescence in *L. musgravei* may have evolved as an adaptation to the alpine environment to insulate against heat loss and protect against high levels of radiation.

Key words: Wolf Spiders, *Artoria alta, Lycosa musgravei,* Australian Alps, pubescence

THE ALTITUDINAL PROFILE of the Australian Alps can be divided into three main ecological zones: alpine, subalpine, and montane (McLuckie & Petrie 1927). The alpine zone includes the area above the physiological limit of tree growth (ca. 1800 m). In the Australian Alps, it has a continuous snow cover for at least four months per year, and for six to eight months the minimum temperature is below freezing. Precipitation is high and ranges from 1,800 – 3,100 mm per year, with about 60% falling as snow (Costin 1957). Herbfields and heathlands dominate the vegetation and approximately 200 species in at least ten different plant communities are recognized (Costin *et al.* 1979). Globally, the alpine zone has its upper limit where there is a permanent cover of snow or ice (nival zone); however, the temperature regime even at its highest elevation at Mt Kosciusko (2,230m) is too warm to establish a nival zone in the Australian Alps. The subalpine zone reaches from the treeline down to the winter snowline, signified by the presence of a continuous cover of snow for at least one month (ca. 1500 m). Minimum mean temperatures below freezing prevail for about six months, and precipitation ranges from ca. 770 – 2200 mm. Snow Gum (*Eucalyptus pauciflora*) dominates the woodland, in addition to wet and dry heathland and sod tussock grassland. The subalpine zone changes into the montane zone (ca. 900 – 1500 m), with the transition from Snow Gum woodland to eucalypt forest (Costin 1975).

Despite a short vegetation period and comparatively harsh conditions, the alpine and subalpine environment host a diverse fauna. In addition to species which extend their range from lower altitudes only in the favourable summer months, some animals facultatively live above the treeline ('eualpine') or at least may be able to complete their whole life cycle there ('tychoalpine') (Hesse 1924; 'alpine residents' in Green & Osborne 1994). Invertebrates, in particular grasshoppers and spiders, show a high number of alpine species in the Australian Alps (Green & Osborne 1994). The diversity of spiders appears to be unaffected by the change from a woodland to treeless alpine environment. About 20 families have been reported to occur in alpine and subalpine regions of the Australian Alps but a large number of species remain undescribed (Green 1988; in Green & Osborne 1994). Wolf spiders (Lycosidae) belong to the better-known taxa, and some appear to be particularly abundant in tall alpine herbfields and tussock grasslands. Three species of lycosids from the alpine region of Mt Kosciusko have been scientifically named: *Lycosa kosciuskoensis* McKay, 1974, *L. summa* McKay, 1974, and *L. musgravei* McKay, 1974, all known from females only. Other lycosids may be found at high altitudes but appear to occur mainly in forests of the montane region, such as *Venatrix funesta* (C. L. Koch, 1847) and *V. australiensis* Framenau & Vink, 2001 (Framenau & Vink 2001).

A number of morphological adaptations found in high altitude arthropods are attributed to alpine environmental conditions (Mani 1968; Somme 1989): Increased hairiness (pubescence) is thought to serve as thermal insulation and protection against ultra-violet light; increased melanism (darkening) may improve heat absorption; and a decrease in size is thought to be due to a shorter time for growth, reduced food availability, and increased shelter options. For example, the Central European wolf spider *Pardosa saturatior* Simon, 1937, which is found above ca. 800 m is darker in colouration than its sibling species *P. wagleri* (Hahn, 1822), which mainly occurs at lower altitudes (Barthel & von Helversen 1990; Manderbach & Framenau 2001). However, *P. saturatior* is significantly larger than *P. wagleri*, contradicting the predictions of Mani (1968) and Somme (1989).

Recent examinations of the collections of the Australian Museum, Sydney, the Australian National Insect Collection, Canberra, and the Museum Victoria, Melbourne, provided new wolf spider material from the alpine zone of the Australian Alps. The aim of this study is to facilitate the identification and study of alpine wolf spiders by describing a new species, *Artoria alta* sp. nov., and illustrating the male of *L. musgravei* of which only the holotype female was known (McKay 1974). In addition, some morphological features of these species are discussed as adaptations to the extreme conditions of the alpine environment.

MATERIALS AND METHODS

Descriptions are based on specimens preserved in 70% ethanol. The epigyne of a female *L. musgravei* was prepared for examination by submersion in 10% KOH overnight at room temperature. For clarity, the illustrations of male and female genitalic organs omit the setae. The morphological nomenclature follows Dondale & Redner (1990), Framenau & Vink (2001), and Framenau (2002).

Abbreviations

Eyes. Anterior (AE), anterior median (AME), anterior lateral (ALE), posterior (PE), posterior median (PME), posterior lateral (PLE). Measurements: total length (TL), carapace length (CL) and width (CW), abdomen length (AL) and width (AW). Genitalia: Male pedipalp: embolus (E), basoembolic apophysis (BEA), median apophysis (MA), palea (PA), subtegulum (STE), tegulum (TEG), terminal apophysis (TA). Female genitalia: copulatory duct (CD), median septum (MS), posterior transverse part (PTP), spermatheca (SP).

Collections

Australian Museum, Sydney (AM); Australian National Insect Collection, Canberra (ANIC); Museum of Victoria, Melbourne (MV).

SYSTEMATICS

Artoria alta, sp. nov.

Figs. 1A-D, 2

Material examined. Holotype. ♀, New South Wales, Mt Kosciusko NP, near Smiggin Holes, 1700 m, alpine moor, 36°24'S, 148°26'E, 7.xii.1994, coll. Daniel Bickel (AM KS44789).

Paratypes. 1 ♀, 1 immature ♀, New South Wales, Mt Kosciusko NP, Spencer Ck near Charlottes Pass, 36°24'S, 148°21'E, 28.xi.1994, coll. Daniel Bickel (AM KS45825).

Diagnosis. The shape of the MA of the male pedipalp of A. alta that has a base with two distinct groves and a triangular apical part is unique within the genus *Artoria*.

Description

Males

Carapace (Fig. 1A). Brown, with a distinct light brown median band narrowing posteriorly, constricted anteriorly of fovea, and with a narrow black median line in head region; indistinct light brown submarginal bands; dark grey radial pattern; carapace covered with short black setae except in median band; two rows of black bristles between PME, one long black bristle between AME, and two long bristles below AE. *Sternum*: Uniformly dark brown and sparsely covered with brown setae and bristles, less dense centrally. *Labium*: Brown, basally dark brown; front end truncate and white. *Chelicerae*: Uniformly dark brown; covered with few white setae and black bristles; three (holotype male four on right) retromarginal teeth, with the median largest, two promarginal teeth, with the apical larger. *Pedipalp* (Figs 1B-D): Cymbium with scopulous setae dorsally in apical half; base of MA with two distinct groves and its apical part tringular; E long and stout, resting in a groove of the sickle-shaped TA (Fig. 1D). *Abdomen*: Brown; indistinct dark median band with darker lateral borders; lanceolate heart mark in anterior half very distinct as a result of a dense cover of white

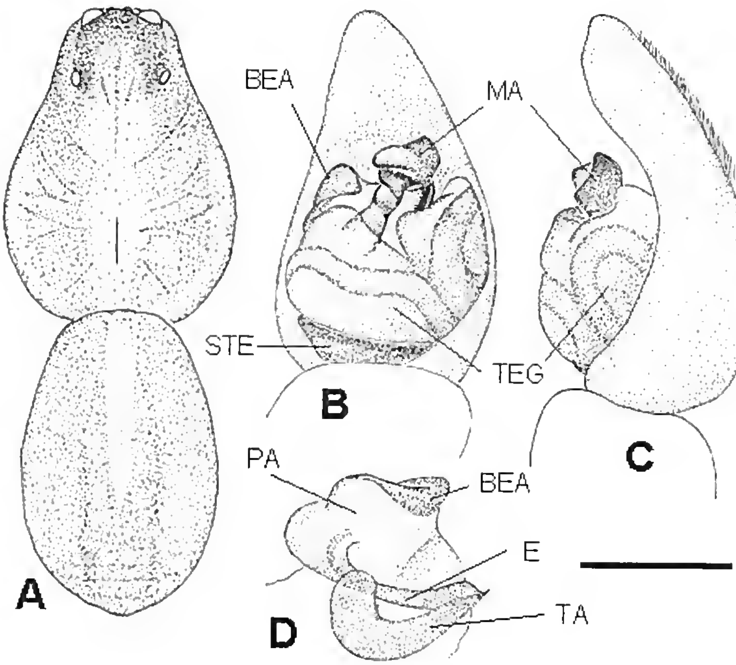

Fig. 1. Male holotype (AM KS44789) of *Artoria alta*, sp. nov.; A, male, *habitus*; B, C, left male pedipalp, ventral and retrolateral view; D, left male pedipalp, apical part of bulbus (MV KS45825). Scale bar: A, 1.5 mm; B, C, 0.34 mm; D, 0.25 mm. BEA, basoembolic apophysis; E, embolus; MA, median apophysis; PA, palea; STE, subtegulum; TA, terminal apophysis; TEG, tegulum.

setae; sparsely covered in white setae and few short, black bristles; venter light brown; setae and bristles as dorsally; spinnerets light brown. *Legs*: Leg formula IV > III > I > II; uniformly brown; spination of leg I: Femur: 3 dorsal, 1 apicoprolateral; tibia: 3 ventral pairs; metatarsus: 3 ventral pairs; 2 prolateral.

Measurements (based on holotype). TL 5.8, CL 3.0, CW 2.2. Eyes: AME 0.09, ALE 0.08, PME 0.3, PLE 0.22. Row of eyes: AE 0.54, PME 0.80, PLE 1.02. Sternum (length/width) 1.4/1.2. Labium (length/width) 0.20/0.20. AL 2.9, AW 1.9. Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 1.0+0.95+ - +0.8 = 2.75, I 2.9+2.4+1.5+0.95 = 6.75, II 1.85+2.25+1.5+1.0 = 6.6, III 1.8+2.0+1.65+0.85 = 6.3, IV 2.3+3.0+2.65+1.15 = 9.1. *Size variation* (male paratype): TL 5.6; CL 2.7; CW 1.85.

Female

Mature female unknown. The colouration of the immature paratype female is similar to the colouration of the male. Its size (TL 6.1, CL 2.55, CW 1.55) suggests a size dimorphism in this species. The female

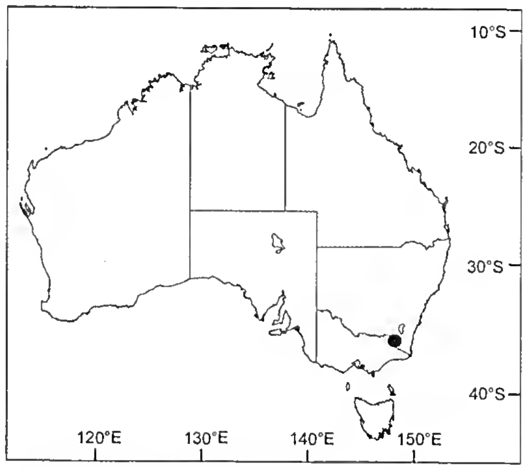

Fig. 2. Records of *Artoria alta*, sp. nov

appears to be larger, as reported in all other species of *Artoria* (Framenau 2002).

Remarks. The genus *Artoria* Thorell, 1877 was recently revised in part to include 12 Australian species, however, more than 50 species may exist (Framenau 2002). The genus is mainly defined by the presence of a broad, basoembolic apophysis (BEA), and the position (apical on tegulum) and shape (spoon-shaped or strongly bifurcate) of the median apophysis of the male pedipalp. The triangular shape of the apical part of the median apophysis of A. alta represents a unique modification of the spoon-shaped form.

The subfamiliar division of wolf spiders remains controversial (e.g., Dondale 1986, Zyuzin 1993, Sierwald 2000, Vink *et al.* 2002). Recent molecular analysis supports the uniqueness of Australasian lycosid genera as suggested by distinct morphological features (Vink *et al.* 2002). In particular the male genital morphology of *Artoria*, as well as of the related New Zealand genera *Anoteropsis* L. Koch, 1878 and *Notocosa* Vink, 2002 (see Vink 2002), does not appear to conform to any of the five main lycosid subfamilies established by Dondale (1986), or the additional Evippinae and Wadicosinae (Zyuzin 1985), Piratinae (Zyuzin 1993), or Tricassinae (Alderweireldt & Jocqué 1993). However, I regard the erection of a new subfamily for *Artoria*, *Anoteropsis* and *Notocosa* premature without further examining the full morphological variation within this group, in particular within the large number of undescribed *Artoria*.

Artoria alta, as inferred from the three specimens examined, does not show any clear morphological adaptations to its alpine habitat. The species is not larger, darker in its colouration (melanism) or has a denser pubescence than any other Australian *Artoria* described (Framenau 2002).

Distribution. Only known from Mt Kosciusko, New South Wales (Fig. 2).

Etymology. The species name is an adjective in apposition derived from the Latin, *altus*, meaning high, and refers to the high altitude at which this species is found.

Lycosa musgravei McKay, 1974
Figs. 3A-G, 4

Lycosa musgravei McKay, 1974: 34-35, Figs 2A-C.- Brignoli, 1983: 450; McKay, 1985: 80.

Material examined. Holotype. ?, *New South Wales, Mt Kosciusko, 36°27'S, 148°16'E, 30.i.1966, L. Voysey (AM KS23).*

Other material examined. **Australian Capital Territory:** 1 female with spiderlings, Mt Gingera, 35°34'S, 148°47'E, 28.v.1970, coll. M. S. Upton, 5800 ft, from silk lined vertical burrow (ANIC); 1 female, Mt Gingera, 35°34'S, 148°47'E, 28.v.1970, coll. M. S. Upton, from silk lined vertical burrow (ANIC); 1 male, Mt Gingera, 35°34'S, 148°47'E, 28.iii.1970, coll. M. S. Upton, 5800ft, free ranging on snow (ANIC). **New South Wales:** 1 female, Bombala, 36°54'S, 149°14'E, i.1930, coll. A. J. Barrett (AM KS84075); 1 male, Charlotte Pass, Mt Kosciusko, 36°24'S, 148°19'E, 8.v.1980, coll. J. Balderson (ANIC); 1 male, 1 female, Crackenback Peak, 36°24'S, 148°32'E, iii.1964, coll. W. A. Howard (ANIC); 2 females, Gungarlin River (tributary of Snowy River), 36°17'S, 148°52'E, no date, coll. R. J. Jenner (AM KS84081); 1 female, Kiandra, 35°52'S, 148°29'E, 21.ii.1960, coll. E. F. Rick (ANIC); 1 female, Mt Kosciusko, 36°27'S, 148°15'E, no date, 6000ft (AM KS84082); 1 male, Mt Kosciusko NP, Wraggs Ck/Pipers Creek Aquaduct, 36°32'S, 148°28'E, 31.iii.1982 (ANIC); 1 female, Perisher Range, East of Guthega Dam, 36°25'S, 148°25'E, 28.i.1962, coll. K. Horne, 5500ft, in burrow (AM KS84079); 1 female, Spencers Creek, Mt Kosciusko, 36°27'S, 148°16'E, 22.xi.1952, coll. A. Musgrave, 1000m (AM KS70010); 1 female, Spencers Creek, Mt Kosciusko, 36°27'S, 148°16'E, 24.xi.1952, coll. A. Musgrave, 1000m (AM KS70012); 1 female, Spencers Creek, Mt Kosciusko, 36°27'S, 148°16'E, 23.xi.1952, coll. C. E. Chadwick, 1000m (AM KS70013); 1 female, Tumut, 35°18'S, 148°13'E, 7.iii.1949, coll. S. Bayliss (AM KS84080); 1 female, Tumut Pond, 35°18'S, 148°13'E, 20.xii.1951, coll. K. R. Sharp (AM KS82593). **Victoria:** 2 females, Elsternwick, 37°53'S, 145°00'E, 20.i.1954, coll. Mr Brownlie (MV K8095, K8209); 3 females, Hotham Heights, 36°59'S, 147°08'E, xii.1933, coll. A. Musgrave (AM KS84076, KS84078); 1 male, Mt Bogong, 36°44'S, 147°18'E, 21.ii.1972, coll. C. Kohlman (MV K8204); 1 male, Mt Bogong, 36°44'S, 147°18'E, 21.ii.1972, coll. C. Kohlman (MV K8207); 1 female, Mt Buffalo, 36°46'S, 146°46'E, xii.1933, coll. A. Musgrave, 4000ft (AM KS84077); 1 female with eggsac (106 larvae, 71 undevelopped eggs), Mt Gibbo, 36°36'S, 147°57'E, 15.i.1975 (MV K8094); 1 female, Mt Hotham, 36°59'S, 147°08'E, i.1945, 6000ft (MV K8205); 1 female, 1 male, Mt Hotham, summit,

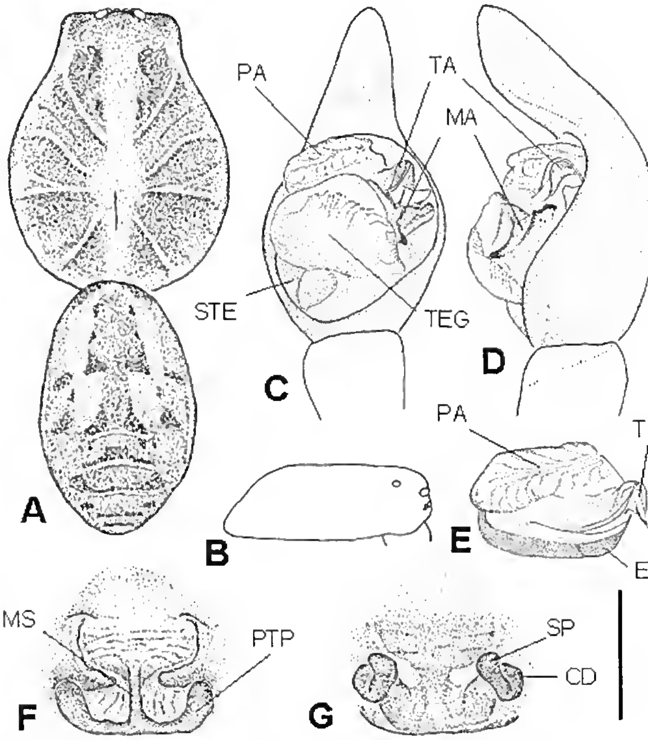

Fig. 3. Male (MV K8204) and female (MV K8095) of *Lycosa musgravei* McKay. A, male, *habitus*; B, carapace, lateral view; C, D, left male pedipalp, ventral and retrolateral view; E, left male pedipalp, apical section of bulbus; F, G, female epigyne, ventral and dorsal view. Scale bar: A, 4.6 mm; B, 6.2 mm; C, D 1.58 mm; E, 1.24 mm; F, G, 1.67 mm. CD, copulatory ducts; E, embolus; MA, median apophysis; MS, median septum of epigyne; PA, palea; PTP, posterior transverse part; SP, spermatheca; STE, subtegulum; TA, terminal apophysis; TEG, tegulum.

36°59'S, 147°08'E, 27.i.1973, coll. M. Pearce, 6100ft, (MV K8206, K8208); 1 female, North Mt Phipps, 1.5km SW Moe, Head of Spring Ck, 37°12'S, 147°26'E, 28.xii.1989, coll. Heath Morris, 4000ft (MV K8166).

Diagnosis. *Lycosa musgravei* is similar in general appearance to *L. gilberta* Hogg, 1905, *L. godeffroyi* L. Koch, 1865 and *L. leuckartii* (Thorell, 1870), three species commonly found in lowland areas of southern and south-eastern Australia (Queensland, New South Wales, Victoria, South Australia, and Western Australia). Males can be distinguished by the shape of the TA, which is double-lamellar in *L. musgravei*, but simply sickle-shaped in *L. godeffroyi* and which forms a wave-like structure in *L. gilberta* and *L. leuckartii*. The lateral tips of the PTP of the female epigyne are strongly curved anteriorly in *L. musgravei*, but point laterally in *L. gilberta*, *L. godeffroyi* and *L. leuckartii*. The abdominal pattern of *L. musgravei* differs distinctly from that of the other two large, alpine lycosids, *L. kosciuskoensis* ('dark brown longitudinal spot surrounded by narrow fawn band that becomes somewhat

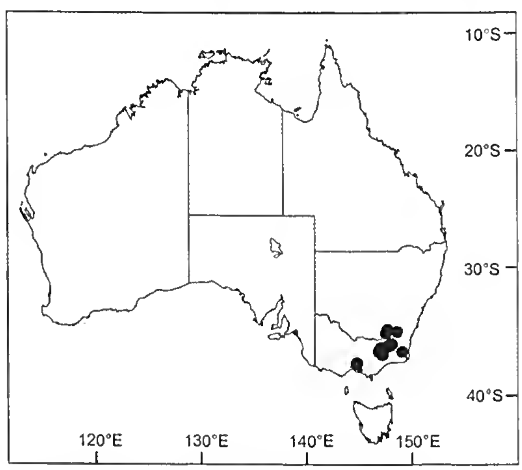

Fig. 4. Records of *Lycosa musgravei* McKay.

diffuse posteriorly') and *L. summa* ('pale brown to fawn (...) longitudinal stripe (...) encloses a dark brown hastate stripe anteriorly') (descriptions cited after McKay 1974; also pers. observation).

Description

Males

Carapace (Fig. 3A-B). Dorsal line in lateral view straight from head region to fovea, then abruptly descending (Fig. 3B); dark reddish brown with light brown median band and four white, but dark edged, radial stripes, the anterior ones reaching below PLE; indistinct light brown submarginal bands; carapace densely covered with short black setae with the exception of head region, median band and light radial stripes which are densely covered with white setae; black bristles in head region and lateral of PLE; one long, black bristle between AME and four long bristles below AE. *Sternum*: Light brown, densely covered with black setae; fewer bristles increasing in length towards margins. *Labium*: Dark brown, front end truncate and light. *Chelicerae*: Reddish brown; densely covered with white setae and fewer black bristles; three retromarginal teeth of similar size, three promarginal teeth with the median largest and the two apical ones fused at the base. *Pedipalp* (Figs 1C-E): Lateral tip of MA with little apical teeth; E broad over all of its length; TA a double lamellar structure with its tip bent basally (Fig. 1E). *Abdomen*: Brown; light brown median band in anterior half contains a double wedge-shaped, dark marking with elongated, black posterior ends; four to five dark chevrons in posterior half; densely covered with setae of variable colour corresponding to abdomen colouration; lateral light brown with dense cover of white setae; venter black with dense cover of black setae; spinnerets dark brown. *Legs*: Leg formula IV > III > I > II; uniformly brown; dense, scopulous setae on all tarsi, metatarsi I and II, and in apical half of metatarsus III and apical third of metatarsus IV; spination of leg I: Femur: 3 dorsal, 2 apicoprolateral, 2 retrolateral; patella: 1 prolateral, 1 retrolateral; tibia: 2 dorsal; 3 ventral pairs, 2 prolateral, 2 retrolateral; metatarsus: 2 ventral pairs; 2 prolateral, 2 retrolateral, 2 small apicoprolateral; 2 small apicoretrolateral.

Measurements (based on MV K8204). TL 18.0, CL 9.9, CW 7.3. Eyes: AME 0.34, ALE 0.35, PME 0.7, PLE 0.60. Row of eyes: AE 1.8, PME 1.9, PLE 2.4. Sternum (length/width) 4.2/3.0. Labium (length/width) 1.1/1.3. AL 3.0, AW 1.8. Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 3.5+3.4+ - +3.8 = 10.7, I 8.0+10.2+7.2+4.1 = 29.5, II 7.4+8.8+6.7+4.0 = 26.9, III 6.5+7.5+6.3+3.7 = 24.0, IV 8.1+10.3+8.7+4.5 = 31.6. *Size variation* (range, mean ± SE): TL 19.0 – 20.6, 19.6 ± 0.9; CL 9.9 – 11.5, 10.7 ± 0.8; CW 7.3 – 8.3, 8.1 ± 0.7; n = 3.

Females

The female of *L. musgravei* is described in detail in McKay (1974). Cephalothorax colouration agrees with that of the male, the abdominal pattern is less distinct. The epigyne of a specimen collected in Victoria is depicted here in ventral (Fig. 3E) and dorsal view (Fig. 3F) to illustrated diagnostic features. Size variation of the material deposited in the MV is given, as only the holotype female was previously known (McKay 1974). *Size variation* (range, mean ± SE): TL 21.0 – 28.5, 24.3 ± 2.8, n = 5; CL 11.0 – 15.0, 12.9 ± 1.3, n = 6; CW 8.3 – 11.1, 9.6 ± 1.1; n = 6.

Remarks *Lycosa* Latreille, 1804 has recently been suggested to be an exclusively Mediterranean genus (Zyuzin & Logunov 2000). In addition, preliminary molecular data suggests that some of the large burrowing lycosids of Australia, of which *L. musgravei* is part of and which were represented in their analysis by *Lycosa godeffroyi*, is close to the North American genus *Geolycosa* Montgomery (Vink et al. 2002). However, the generic description of *Geolycosa* does not match the Australian species (e.g. Dondale & Redner 1990): the dorsal profile of the carapace of *Geolycosa* is highest in the caput region, followed by a gentle slope towards the posterior cephalothorax margin, whereas the dorsal profile of *L. musgravei* is straight over most of the carapace and descends sharply behind the fovea (Fig. 3B). In addition, *Geolycosa* does not have light median and submarginal bands and a Union-Jack-pattern of white radial bands on the carapace which are present in *L. musgravei*, *L. gilberta*, *L. godeffroyi* and *L. leuckartii*. Three recent revisions of Australasian lycosid genera, *Allotrochosina* Roewer, 1960, *Artoria* Thorell, and *Venatrix* Roewer, 1960, suggest the uniqueness of the Australasian fauna (Vink 2001; Framenau & Vink 2001; Framenau 2002). Likewise, *L. musgravei*, and all other Australian lycosids placed in Lycosa, almost certainly belong to different, most likely new genera; however, *L. musgravei* is retained in *Lycosa* pending a full generic revision of Australian wolf spiders, which is currently

being conducted by the author at the Western Australian Museum.

The whole body of *L. musgravei* is covered with a very dense layer of setae and bristles, which are much denser than in any of the specimens of the related species *L. gilberta*, *L. godeffroyi* or *L. leuckartii*, (pers. observation). This dense pubescence conforms to one of the adaptations of high altitude arthropods to insulate against heat loss and protect against high levels of radiation (Mani 1968, Somme 1989).

Habitat and phenology. *Lycosa musgravei* is reported to be the most frequently observed wolf spider in the Snowy Mountains, with their open burrow found in tall alpine herbfields and grasslands (Green & Osborne 1994). The burrow (closed with a thick sheet of webbing in winter) is raised above ground level by inclusion of an open turret of web and vegetation litter (Green & Osborne 1994). The records of two females from Elsternwick (suburban Melbourne) seem to be unusual for this apparently alpine spider, and may be the result of human recreational activities.

Mature females were found from November through to May with the exception of April, with most records in December and January. One female with eggsac and a female carrying young were collected in December and May respectively. Mature males were found between January and May, with the exception of April as in females.

Distribution

Australian Capital Territory, New South Wales and Victoria (Fig. 4).

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GLAUCODON BALLARATENSIS (MARSUPIALIA, DASYURIDAE), A LATE PLIOCENE 'DEVIL' FROM BATESFORD, VICTORIA.

W. R. GERDTZ & N. W. ARCHBOLD

School of Ecology and Environment, Melbourne Campus, Deakin University, Burwood, Victoria, 3125

GERDTZ, W. R. & ARCHBOLD, N. W., 2003:11:30. *Glaucodon ballaratensis* (Marsupialia, Dasyuridae), a late Pliocene 'devil' from Batesford, Victoria. *Proceedings of the Royal Society of Victoria* 115(2): 35-44. ISSN 0035-9211.

The right mandible of a dasyurid from Pliocene sediments at Batesford, near Geelong, Victoria is described as a new specimen of *Glaucodon ballaratensis* Stirton, 1957. The new specimen is morphologically close to the holotype of *Glaucodon ballaratensis*. Several dental characteristics of the new specimen unknown from the holotype of *Glaucodon ballaratensis* are close to those of *Sarcophilus moornaensis* Crabb, 1982. *Glaucodon ballaratensis* also shares features with *Dasyurus maculatus* Kerr, 1792 and *Sarcophilus laniarius harrisii* Boitard, 1842, and hence the Batesford specimen offers additional information on the origins of these dasyurids.

Key words: *Glaucodon ballaratensis*, Pliocene, Batesford, Moorabool Viaduct Sands, Dasyuromorphia, Dasyuridae.

THE DASYUROMORPHIAN fossil record represents the dominant marsupial insectivore-carnivore radiation in Australasia during the Quaternary. Discoveries from Late Oligocene and Miocene deposits in Riversleigh in northwestern Queensland have extended this record (Wroe, 1998), and Wroe (2003) provides a modern summary of fossil Dasyuromorphian record. However, the order is poorly represented in the Pliocene, where the species *Glaucodon ballaratensis* Stirton, 1957, *Dasyurus dunmalli* Bartholomai, 1971, *Archerium chinchillaensis* Wroe & Mackness 2000 and *Sarcophilus moornaensis* Crabb, 1982 are the only known dasyuromorphians. The Pliocene record may also include indeterminate species of *Antechinus* from Grange Burn, Victoria (Turnbull & Lundelius, 1970), and *Planigale* from Bluff Downs in Queensland (Archer, 1982).

The monotypic genus *Glaucodon* was described by Stirton (1957) and based on a single right mandible with the M4 present. The holotype was found in the Parish Well at Smeaton, near Ballarat. The specimen was originally presented to the National Museum of Victoria in 1914 by Mr. J. Marshall, and remained undescribed for over forty years. E. D. Gill revisited the type location and discovered the first molar (M1) which fits into the alveolus and contacts perfectly with the broken root of the posterior alveolus (Gill, 1953). The holotype of *Glaucodon ballaratensis* (NMV P16136) therefore includes the remains collected by both Marshall and Gill. In 1964, W. D. Turnbull recognised two fragments in the Museum Victoria Vertebrate Palaeontology Collections as coming from the well at Smeaton that belonged to the holotype of *G. ballaratensis*. Together the fragments provide much of the outline of the ascending ramus from the left dentary. This material was not available to Stirton (1957) when the holotype was first described.

Stirton did not assign *G. ballaratensis* a geological age with any certainty. Gill's analysis of the sediments surrounding the supplementary material collected in 1953 indicated that the specimen's stratigraphical position in the section at Smeaton can be established relative to the overlying basalt flows (Gill, 1953). Another analysis of the Smeaton locality undertaken in 1993 noted that the fossiliferous layer that contained *G. ballaratensis* lies above a basalt flow which correlates closely with a nearby flow with a radiometric date of 2.1 myBP (Turnbull, Lundelius & Tedford, 1993). Basalt flows above the fossiliferous layer have been interpreted as no older than 1.9 myBP (Aziz-ur-Rhaman & McDougall, 1972). This implies that the sediment containing *G. ballaratensis* represents an interval between basalt flows of the ages of 1.9 myBP and 2.1 myBP, which implies a Late Pliocene age for the holotype.

The right mandible of a fossil dasyurid with near complete dentition (NMV P207018) was presented to

the Museum of Victoria in 1996 by Mr. P. Robertson. Robertson's specimen was found in the Moorabool Viaduct Sands (Pliocene) outcropping at Portland Cement Limited's Limestone quarry at Batesford, Victoria. The specimen was referred to *G. ballaratensis* (T. H. Rich, pers. comm. 1997, see Gerdtz, 2001). Morphological characteristics of the teeth of this specimen fully confirm that the specimen belongs to this species. Measurements and comparisons of the teeth and mandible of Robertson's specimen reveal differences in relative proportions of the molar trigonids and mandibular depth to those of the holotype, however the differences are considered to be of infraspecific importance.

The significance of *G. ballaratensis* in dasyuromorphian evolution has been discussed by Gill (1953), Stirton (1957), Ride (1964). Marshall (1973), Archer (1976, 1982), Archer and Bartholomai (1978) and Crabb (1982). Characteristics of the Batesford specimen offer additional information on the phylogeny of the Dasyuridae, specifically the relationship of *Glaucodon* to *Dasyurus maculatus* Kerr, 1792, *Sarcophilus laniarius harrisii* Boitard, 1842 and *Sarcophilus moornaensis* Crabb, 1982.

STRATIGRAPHY AND AGE OF THE BATESFORD SPECIMEN

It has been suggested (T. H. Rich, pers. comm.) that the distinctive preservation of the Batesford specimen of *G. ballaratensis* indicates that it was originally located in a fissure filling within the argillaceous Moorabool Viaduct Sands of Pliocene age. The unit, as exposed at Batesford Quarry, consists of a black, silty clay with a notable absence of finely comminuted marine fossils (Rich, 1976). The dark brown coloration of the mandible and black coloration of the tooth enamel of the specimen corresponds with other vertebrate remains attributed to this unit, notably a *Zygomaturus* sp. mandible found in these sediments at Batesford in 1975 (Rich, 1976). This unit has yielded a substantial list of fossilized remains known as the Dog Rocks Local Fauna, including marsupials and other mammals such as Rodentia (Muridae), along with representatives of Osteichthyes (Teleosti), Amphibia (Anura), Reptilia (Squamata), and Aves (Rich, 1991).

The sediments of this unit indicate a fluviatile environment existed to the southeast of the Dog Rocks during the Pliocene. It is the characteristic preservation of the Dog Rocks local fauna, along with information provided on the location of the new specimen by Robertson that led T. H. Rich to his assessment that the specimen came from this setting. The fossiliferous unit of the Moorabool Viaduct Sands was overlain by a number of basalt flows of the Newer Volcanics (Bowler, 1963). Three kilometres to the south of Batesford Quarry, a magnetically reversed flow with similar petrographic characteristics was dated at 2.03 +/- 0.13 my BP in three different samples (Aziz-ur-Rahmen & McDougall, 1972). A determination for the maximum age of the fluviatile sediments was provided by the foraminiferan *Globoratalia crassiformis*, which first appeared at 4.0 myBP (Whitelaw, 1989) and occurs in the sediments of the Moorabool Viaduct Sand stratigraphically below the fissures. In these sediments, the magnetic orientation is reversed (Whitelaw, 1989) which suggests that the age of the fissures is within the interval of 4.0 and 1.9 myBP, thus placing it in either the early Matayuma Chron (2.48-2.03 myBP) or the late Gilbert Chron (4.88-3.40 myBP)(Aziz-ur-Rahmen & McDougall, 1972). The presence of rodents in the local fauna such as the two identified *Pseudomys* species suggests that the early Matayuma Chron is the most likely interval represented in these sediments (Whitelaw, 1989).

SYSTEMATIC PALAEONTOLOGY

Subclass MARSUPIALIA Illiger, 1811

Cohort AUSTRALIDELPHIA Szalay, 1982

Order DASYUROMORPHIA Gill, 1872

Family DASYURIDAE Goldfuss, 1820

Genus **Glaucodon** Stirton, 1857

Type species *Glaucodon ballaratensis* Stirton, 1857

Holotype. The diagnostic features of the holotype of *G. ballaratensis* (NMV P 16136) were defined as the following: Molar row length intermediate between *Dasyurus maculatus* and *Sarcophilus laniarius harrisii*; gross morphology of mandible less robust than *Sarcophilus* form but more so than *D. maculatus*; M4 length of 10.0 mm +/- 0. 1 mm: M4 width 6.7 mm +/- 0.4 mm; M1 length 7.2 mm +/- 0.5 mm; M1 width 4.3 mm +/- 0.2 mm (Stirton, 1957).

The dental morphology of the holotype of *G. ballaratensis* (NMV P16136) has been discussed by

Gill (1953), Stirton (1957), Ride (1964), Marshall (1973), Archer (1976, 1982), Archer and Bartholomai (1978), Crabb (1982) and Long et al. (2002). It was fully described by Stirton (1957) based on a solitary right mandible with M1 and M4 present, and alveoli for M2, M3, P1, P2, C, and an incomplete row of incisor alveoli. Gill (1953) postulated in his field notes, but did not formally describe, the specimen as a member of the genus *Sarcophilus*. *G. ballaratensis* is regarded herein as a morphologically intermediate form between *Sarcophilus laniarius harrisii* and *Dasyurus maculatus*, displaying characteristics referable to both species. Stirton (1957) also noted some dental morphological similarities between G. ballaratensis and *Dasyurus viverrinus* (Shaw, 1800), however the similarities were less marked than those of *D. maculatus*.

Glaucodon ballaratensis Stirton, 1957
Fig. 1, 2, 3

Sarcophilus? Gill, 1953, p. 87

Glaucodon ballaratensis Stirton, 1957, p. 129-133, text-figure 6.

Glaucodon ballaratensis Stirton, 1957, - Archer, 1984, p. 634, Table 1; p. 635, fig 2; p. 639, fig 17; p.640, fig. 18; . Pl. 6.7-1. - Crabb, 1982, p. 514 - 515, fig 4, - Archer, 1982, p. 409, fig 7, p. 417. - Ride, 1964, p. 109, fig 8; Long et al., 2002, p. 55, fig p. 53 (mislabelled as *Dasyurus dunnalli*)

New material. NMV P207018. As for *G. ballaratensis* holotype (NMV P16136), with the following additional features: Mandible with four molars (M1, M2, M3 and M4) in situ, however the protoconid of M4 is absent, possibly due to

Fig. 1. NMVP 207018, occlusal view. Scale bar intervals represent 10mm.

postmortem abrasion. Also present are two well-spaced premolars (P2 and P3) and a large crescentic canine. Occlusal surfaces are relatively unworn, suggesting that the specimen was a young adult. The mandible of the specimen is somewhat shorter and more robust than holotype.

Locality of new material. Specimen found by P. Robertson in the Moorabool Viaduct Sand, a member of the Brighton Group (Pliocene), at Portland Cement Limited's limestone quarry at Batesford, Geelong, Victoria (38° 6.5' S., 144° 17.5' E).

Diagnosis of species. Diagnostic features are: deep, channel-like precingulum extending to the parastylid on M2, M3 and M4 (precingulum on M1 present but less markedly) consistent with 'bone cracking' dasyurids; more robust trigonids than holotype (M1 trigonid longer, M4 trigonid both longer and wider); crowding of molar row out of line comparable to holotype (and *S. moornaensis*, but significantly less than *S. laniarius harrisii*); talonid-like notch in anterior base of P2 undercuts and is rectilinear to the protoconid. premolar diastema intermediate between *D. maculatus* and *S. laniarius harrisii* and referable to alveoli on *G. ballaratensis* holotype; P1 significantly lower than P2 with rounded, low cusp. The mandible is more robust and deeper than holotype, deepest beneath the M4 between roots.

Measurements were taken from twenty specimens each of *D. maculatus* and *S. laniarius harrisii*, as well as the holotypes of *S. moornaensis* (NMV P28684) and *G. ballaratensis* (NMV P16136) to provide a morphometric comparison of twenty-eight dental and mandibular characteristics against the new specimen (Table 1). Measurements from the canine are discarded as being diagnostic because of wear via occlusion. The parameters of variability of the measurements of the talonid and trigonid basins of the M2 and M3 are not used as a diagnostic feature from the holotype, as these teeth are represented by alveoli only.

NMV P207018 differs from the holotype of *G. ballaratensis* in the following characteristics: more robust mandible, mandibular depth beneath P2 deeper

Fig. 2. NMVP 207018, lingual view. Scale bar intervals represent 10mm.

and closer to the mandibular depth proportions displayed in *S. moornaensis*, M1 and M4 wider.

NMV P207018 shares the following features with the holotype: molar talonids weaker and more adpressed than *Sarcophilus*, but less so than *Dasyurus*, molar protoconids high and sharp, particularly on M3 and inferred on M4, molar row length and crowding intermediate between *S. moornaensis* and *D. maculatus*.

It has been suggested that Robertson's specimen may represent an ontogenetically older individual of *G. ballaratensis* (G. D. Sanson, pers. comm., 1999). Whilst this addresses the apparent crowding of the molar row of the illustrated specimen (as a result of interstitial wear), the occlusal wear patterns on the protoconid and the hypoconid of the M1 of NMV P 207018, unknown to Sanson, suggest it was of similar or younger ontogenetic age than the holotype. The observed differences in dental morphology between the two specimens, however, provide insufficient evidence for the existence of two species of *Glaucodon*.

Morphometric analyses set forth by Simpson, Roe & Lewontin (1960) were used by Marshall (1973) to synonymise *G. ballaratensis* with a specimen from the Moorna Sands, South Australia. This diagnosis was later re-examined by Crabb (1982) using morphological observations, and the Moorna Sands specimen was erected as the holotype of *Sarcophilus moornaensis*. This suggests that Simpson's form of analysis is problematic when morphological observations are not included in the statistical analysis. It is pertinent to note that data derived from Simpson's approach implied the presence of two species of *Glaucodon* on the basis of dental measurements (Table 2) when comparing the *Glaucodon* specimens.

The present authors consider that it is therefore necessary to incorporate both observations of morphology and dental measurement statistics concurrently to diagnose this species from other morphologically similar taxa.

Description of NMV P207018. Dentition more complete than holotype (NMV P16136), however, ramus length and length of molar row is marginally shorter,

Fig. 3. NMVP 207018, labial view. Scale bar intervals represent 10mm.

CHARACTER	*Dasyurus maculatus* (n) = 20	*Sarcophilus laniarius harrisi* (n) = 20	*Sarcophilus moornaensis* (n) = 1	*G. ballaratensis* holotype MV P16136 (n) = 1	*G. ballaratensis* MV P702018 (n) = 1
Length of molar series	27.7 +/- 3.8	44 +/- 4.7	38.5	36.4	35
M1 length	7.7 +/- 2.1	9.2 +/- 2.6	7.8	7.4	6.5
M1 width	3.7 +/- 1	6.2 +/- 2.5	5.2	4	4.5
M1 trigonid length	2.7 +/- 1.2	7 +/- 3.2	7.2	4.3	4.7
M1 trigonid width	1.8 +/- 0.8	4.5 +/- 1.7	5	4.3	4.3
M1 talonid width	2.1 +/- 1	4.9 +/- 2.2	3.2	4.5	4.3
M2 length	6.5 +/- 1.7	10.9 +/- 2.9	9.5	absent	8.6
M2 width	3.4 +/- 1	6.5 +/- 1.8	5.9	absent	4.8
M2 trigonid length	3.3 +/- 1.3	8.4 +/- 2	8.7	absent	6.1
M2 trigonid width	3.4 +/- 1.2	5.2 +/- 3.7	3.8	absent	4.9
M2 talonid width	3.1 +/- 1	3.3 +/- 1.8	4.5	absent	5.2
M3 length	6.7 +/- 2.2	12 +/- 2.7	10	absent	9.8
M3 width	3.9 +/- 1.9	7.4 +/- 1.5	6.3	absent	6.7
M3 trigonid length	3.6 +/- 1.8	7.7 +/- 1.8	8	absent	7.6
M3 trigonid width	3.6 +/- 1.4	5.6 +/- 1.4	5.4	absent	5.2
M3 talonid width	2.8 +/- 1.2	2.3 +/- 2.1	3.3	absent	4.4
M4 length	6.8 +/- 2.3	11.9 +/- 3.6	11.2	10	10.1
M4 width	3.7 +/- 1.6	6.5 +/- 2.1	6.5	5.8	6.3
M4 trigonid length	4.4 +/- 1.3	9.9 +/- 1.2	10.2	6	8.2
M4 trigonid width	3.7 +/- 1.2	4.8 +/- 1.4	4.6	3.3	5.6
M4 talonid width	2.9 +/- 1	2.3 +/- 1.8	2.9	2	2.1
P2 length	4.2 +/- 1.7	6 +/- 2.7	absent	absent	4.3
P2 width	3.2 +/- 1.3	6.7 +/- 2.3	absent	absent	3.5
P3 length	4.9 +/- 2.1	6.7 +/- 2	absent	absent	5.9
P3 width	2.9 +/- 1.1	6.5 +/- 2.2	absent	absent	3.9
Mandible depth below P2	10.6 +/- 2.3	12.4 +/- 3.4	14.6	10.1	12.2
Mandible depth below M4	15.1 +/- 3.1	12.3 +/- 2.8	20	17.5	17.1
Mandible depth below M1	14.1 +/- 3.8	13.8 +/- 3	14.7	13.7	13

Table 1. Mean dental measurements from subjective and comparative material

incisor alveolus not present due to incomplete preservation of specimen. Premolars in line with significant spacing, canine relatively robust and crescentic. P1 is set oblique to antero - posterior axis of tooth row and P2 is only slightly so. Molars characterized by deep, channel-like precingulum extending to the parastylid.

M1 short but wide; heavy median protoconid; anterior median crest from base to top of protoconid; metaconid tightly adpressed to posterolingual slope of protoconid; hypoconid massive and slightly crescentic; hypoconulid in posteromedian position at posterior end of hypoconid crescent; entoconid as small rounded cusp; talonid basin with narrow lingual opening anterior and posterior to entoconid - no direct posterior opening; posterior lower labial corner extends farther posteriorly than other parts of the tooth; trigonid long and deep; paraconid obscure due to massive nature of protoconid.

M2 with moderate paraconid - protoconid shear; protoconid higher than paraconid, separated by carnassial notch; protoconid with posteriorly oriented curvature, inner lingual surface flattened; metaconid much lower than protoconid but only marginally shorter that paraconid; talonid basin comparatively large, high and shallow with wider lingual opening posterior to entoconid and small posterior opening; margin of talonid with entoconid only marginally lower than hypoconid; posterior lower labial corner marginally extends further posteriorly than other parts of the tooth; trigonid basin high and shallow.

M3 with high sharp paraconid - protoconid shear; protoconid higher than paraconid, separated by carnassial notch along paracristid; protoconid high with crescentic distally oriented curve, noticeable groove along labial aspect of metacristid; metaconid lower than protoconid but roughly the same height as paraconid; protoconid higher than paraconid.

M4 wide; protoconid absent, possibly due to abrasion; remains of high paraconid - protoconid shear surface evident; partial protoconid and paraconid separated by a carnassial notch in the paracristid; metaconid lower than paraconid; trigonid basin wide and shallow. The trigonid length compared to the total length of the molar is large, and is a characteristic of this species not shown in the comparative material of *D. maculatus*, *S. harrisii* and S. *moornaensis*.

Paraconid and metaconid progressively enlarge from M2 to M4, however talonid remains adpressed in each case. Remains of the incomplete M4 protoconid suggests it was higher than paraconid with marginally adpressed talonid present.

P2 composed of single high anterior cusp with angular posterior slope to mandible attachment longer than anterior slope; anterior attachment to mandible separated by notch in base in line with single high cusp. P1 much lower than P2; cusp barely discernible on worn surface; anteriorly well spaced from P2 but crowded in line with C.

C high and crescentic; slight lingual slope; single rounded high cusp; anteriolingual surface marked by vertical groove.

Discussion of phylogeny of Glaucodon Considerable discussion on the phylogeny of *Glaucodon* exists. Marshall (1973, p. 156) considered that there was an absence of morphological differences between *G. ballaratensis* and *S. moornaensis*, and hence synonymised the two species. The methodologies of Simpson, Roe & Lewontin (1960) were applied as a basis of dental morphometric analysis in this instance. While there are distinct morphological similarities between *Glaucodon* and *Sarcophilus*, specimens of the latter are larger and more robust, with a significantly greater mandibular depth and crowding of the molar row.

Ride (1964) proposed that *G. ballaratensis* was structurally ancestral to *S. harrisii*, but in some characteristics closer to larger species of *Dasyurus* such as *D. maculatus*. This suggestion implies *Glaucodon* is ancestral to *Sarcophilus* with some characteristics referable to *Dasyurus*. The phylogenetic relationships of *Dasyurus* and *Sarcophilus* have been established by molecular studies indicating that the genera form a monophyletic group (Krajewski et al., 1994). It is noteworthy that more recent molecular data is not in accord with this interpretation (Krajewski et al., 2000), but more recent morphology-based numerical parsimony supports the case for monophyly of this taxa (Wroe et al., 2000). This demonstrates the significance of morphology in the elucidation of phylogeny in extant taxa. Archer and Bartholomai (1978, p. 5) recognized "a structural lineage starting with a hypothetical fossil form similar to *D. maculatus*, to *G. ballaratensis*, to the annectant extinct species of *Sarcophilus* and ending with *S. harrisii* is one of the best documented marsupial structural phylogenies", where the annectant species mentioned is *S. moornaensis*. Wroe (1998) discussed the phylogeny of this lineage from the perspective of an ancestral Miocene dasyurid, *Ganbulanyi djadjinguli* Wroe, 1998, noting synapomorphies of *Dasyurus*, *Glaucodon* and *Sarcophilus*.

Crabb (1982) considered the lower molars of S.

moornaensis similar to (and as apomorphic as) the molars of *G. ballaratensis*. The mandibular depth and crowding of the molar row of *S. moornaensis* is greater than that of both specimens of *Glaucodon*, however this characteristic is less marked in the Batesford specimen. The more robust trigonids of the M1 and M4 and the mandibular depth of the Batesford specimen differ from the *G. ballaratensis* holotype, however these differences are regarded as being of infraspecific importance. It is important to consider, when discussing the relationships of the *Glaucodon-Dasyurus-Sarcophilus* lineage, the relative ages of all the taxa involved. *S. moornaensis* is considered Early Pleistocene in age (Long et. al., 2002). The revised estimation of the geological age of the holotype of *G. ballaratensis* (2.0 myBP +/- 0.1 myBP) removes the importance of the specimen in 'stage-of-evolution' correlation for this group of dasyurids. as the occurrence of the species is too recent to constitute 'common ancestry' (Turnbull, Lundelius & Tedford, 1993). However, the morphology of the teeth attributed herein to *G. ballaratensis* combined with the estimated geological age of NMV P207018 (2.2 myBP +/- 0.25 myBP) raises the significance on the species in terms of 'stage-of-evolution' correlation. *G. ballaratensis* can now be regarded as representing a collateral lineage to *Sarcophilus*. The retention of characteristics such as the gracile mandibular form shared by *Glaucodon* and *Dasyurus* are considered symplesiomorphic.

The dental and mandibular characteristics of NMV P207018 provide new data on *Glaucodon* and the characteristics that it shares with *Sarcophilus*. *G. ballaratensis* is a Pliocene form that, whilst sufficiently different to warrant generic distinction from the Dasyurinae and *Sarcophilus*, has characteristics allying it with these taxa. The molar row crowding and proportions of the M4 trigonid of NMV P207018 implies a closer affinity between the genera *Glaucodon* and *Sarcophilus* than previously postulated. The poorly developed molar talonids of NMV P207018 align the specimen with Glaucodon rather than Sarcophilus. The robust molars of the Batesford specimen are morphologically intermediate between the holotype of *G. ballaratensis* and *S. moornaensis*. However, these differences are likely to represent intraspecific variation within *G. ballaratensis* rather than a new species of *Glaucodon*.

A possible interpretation of the phylogeny of the lineage is as follows: at some point prior to the late Pliocene, the Dasyurinae diversified resulting in the origin of the *Sarcophilus-Glaucodon* lineage. The plesiomorphic gracile morphology and uncrowded molars of the ancestral form were retained and are present in extant species of *Dasyurus*. The *Sarcophilus-Glaucodon* lineage retained some elements of the dental arrangement of the ancestral form. However, significant progressive crowding of the molar row is an evident apomorphy of the subfamily as displayed in *S. laniarius harrisii*.

Glaucodon branched from the *Sarcophilus-Glaucodon* lineage after the split from the Dasyurinae, but prior to the occurrence of *S. moornaensis*. *G. ballaratensis* arose at some point prior to the Late Pliocene, and retained the symplesiomorphic proportions present in the mandible of *D. maculatus*, but also displayed characteristics which unite it with *Sarcophilus*. A characteristic of *Sarcophilus* is the gradual increase of morphological robustness through the Plio-Pleistocene *S. moornaensis* to the massively

CHARACTER	*G. ballaratensis* holotype MV P 16136	*G. ballaratensis* MV P 702018	Log. difference	Nearest whole number value for V	Indicative of new species ?
Length of molar series	34.4	35	0.0076	<1	N
M1 Length	7.4	6.5	0.056	3 to 4	Y
M1 Width	4	4.5	0.0511	3 to 4	Y
M1 Trigonid length	4.4	4.7	0.029	1 to 2	N
M1 Trigonid width	4.3	4.3	nil	N/A	N
M1 Talonid width	4.5	4.3	0.03	1 to 2	N
M4 Length	10	10.1	0.004	<1	N
M4 Width	5.8	6.3	0.0359	2 to 3	N
M4 Trigonid length	6	8.2	0.1356	7 to 8	Y
M4 Trigonid width	3.3	5.6	0.2297	12 to 13	Y
M4 Talonid width	2	2.1	0.0212	1 to 2	N
Mandible depth below P2	10.1	12.2	0.082	4 to 5	Y
Mandible depth below M4	17.3	17.1	0.0051	<1	N
Mandible depth below M1	13.5	13.2	0.0097	<1	N

Table 2. Application of morphometric analysis of Simpson et al. (1960) to *Glaucodon*. (Note: values for V greater than 3 indicate a different species. Chronology and phylogeny are not applied in this approach to species differentiation.)

robust *S. laniarus* complex of the Pleistocene. Future discoveries from these theorised lineages could add to the understanding of the evolution of the Dasyuridae in the Plio-Pleistocene.

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AN EARLY OCCURRENCE OF *SARCOPHILUS LANIARIUS HARRISII* (MARSUPIALIA, DASYURIDAE) FROM THE EARLY PLEISTOCENE OF NELSON BAY, VICTORIA.

W. R. GERDTZ & N. W. ARCHBOLD

School of Ecology and Environment, Melbourne Campus, Deakin University, Burwood, Victoria, 3125

GERDTZ, W. R. & ARCHBOLD, N. W., 2003:11:30. An early occurrence of *Sarcophilus laniarius harrisii* (Marsupialia, Dasyuridae) from Nelson Bay, Victoria. *Proceedings of the Royal Society of Victoria* 115(2): 45-54. ISSN 0035-9211.

The isolated lower molar series of a dasyurid from early Pleistocene sediments at Nelson Bay, near Portland, is referred herein to *Sarcophilus laniarius harrisii* (Boitard, 1842). Dental measurements and morphological comparisons taken from this tooth series compare closely with those of the extant subspecies. The genus *Sarcophilus* is known from the early Pleistocene by the species *S. moornaensis* Crabb 1982. Fossil material assigned to *S. laniarius harrisii* is now also known from Early Pleistocene sediments. The new specimens from Nelson Bay extend the origin of *S. laniarius harrisii* to the early Pleistocene.

Key words: *Sarcophilus laniarius harrisii*, Pleistocene, Portland, Nelson Bay Formation, Dasyuromorphia, Dasyuridae.

THE FIRST reports of the occurrence of the fossil remains of the living Tasmanian *Sarcophilus* in the Quaternary deposits of Victoria were by Selwyn (1858, 1860) based on identifications by Frederick McCoy. The modern geographical distribution of the extant dasyurid subspecies *Sarcophilus laniarius harrisii* (Boitard, 1842) widely known as *S. harrisii* (Boitard 1842) is restricted to dry sclerophyll forests and coastal woodlands of Tasmania (Strahan, 1995). The fossil record of the species has a distribution on mainland Australia during the Pleistocene (Long et. al. 2002). Fossil *S. laniarius* has been recorded in many geochronologically dated Pleistocene and early Holocene terrestrial and cave fossil localities. Representative occurrences are provided in Table 1. The maximum range of the geochronologically dated specimens is no older than 0.352 +/- 1.8 Mya down to less than 10,000 years. The extinction of the species from the mainland is believed to have been the result of a failure of the species to compete successfully with the introduced Dingo *Canis familiaris dingo* (see Corbett, 1985), which occupied a comparable ecological niche (Strahan, 1995).

The earliest occurrence of *Sarcophilus* is from the early Pleistocene, with *S. moornaensis* Crabb (1982), known from a right mandible and molars, and is a member of the Fisherman's Cliff Local Fauna (Crabb, 1982). Crabb's species comes from the sands of the Moorna Formation in south western New South Wales, which is estimated to be early Pleistocene in age (Long et. al. 2002). Late Pleistocene fossil-bearing deposits in the Wellington Caves, New South Wales have yielded significantly larger specimens of *Sarcophilus*, and the species *S. laniarius* (Owen, 1838) was proposed for this material. Werderlin (1987) argued strongly that *S. laniarius* is the senior synonym for *S. harrisii*, and recognised three subspecies of *S. laniarius*, namely *S. laniarius laniarius* (Owen, 1838), *S. laniarius dixonae* (Werderlin, 1987) and *S. laniarius harrisii* (Boitard, 1842), the latter of which is also the extant subspecies. Dawson (1982) recognised the basis for diagnostic distinction of *S. laniarius laniarius* from the extant species is the larger size rather than discrete morphological differences. Murray (1991) noted that the Wellington Caves *S. laniarius laniarius* is an "essentially statistically assigned (sub) species (with) no particular morphological features other than significantly larger size and associated allometry from ...present-day Tasmanian Devils" (Murray, 1991, p. 1090-1091). As a result we accept that *S. laniarius laniarius* is a larger form of *S. laniarius harrisii*. For the purposes of this present report, we follow Werderlin's (1987) taxonomy of the three subspecies, and the binomen *S. laniarius* (Owen, 1838) has priority, as shown in Long et al. (2002).

It may be argued that the use of *S. laniarius* (Owen, 1838) as the senior synonym of *S. harrisii* (Boitard, 1841) for the living Tasmanian Devil results in the destabilization of commonly used nomenclature. While Environment Australia's biodiversity fauna list

(Environment Australia, Australian Biological Resources Study, 2002) refers to *S. harrisii* as the binomen for the living species, it is in contrast with Smithsonian Museum of Natural History taxonomic database (Smithsonian Museum of Natural History, Department of Systematic Biology, 1993) that recognizes the priority of *S. laniarius* for the extant species. As shown by Werderlin (1987) and subsequent workers (Long *et. al.* 2002), this recognition of priority does not significantly destabilize nomenclature and is therefore retained by us.

In the late 1970's, a stratigraphical review of the sediments outcropping in Nelson Bay, near Portland, was undertaken by E. D. Gill, C. W. Mallett, J. M. Lindsay and N. W. Archbold. Archbold collected a small collection of fossil bone and tooth material from a single locality. Amongst the collected material were assorted diprotodontid, vombatid, macropodine and dasyurid mandibular and dental remains. It is the dasyurid material that is described herein and is assigned to *S. laniarius harrisii* on the basis of dental measurements and morphology. Due to the age of the sediments that contained this material (0.73 - 1.66mya) (White, 2002), it appears that they constitute the earliest occurrence of this species.

Stratigraphy and age

Based on field notes and personal recollections from one of us (N. W. A.) relating to the locality, the unit in which the material is referred to is unquestionably the Nelson Bay Formation, located approximately 5 km south of Portland (38° 36' S., 141° 35' E.). Studies of the sedimentary processes and the formation of the bone beds which outcrop at Nelson Bay have been undertaken by Boutakoff (1963) and Kenley (1988), and were reviewed by White (2002).

The sediments of the Nelson Bay Formation were deposited in a lacustrine environment that existed at this locality at the time of deposition. The lake occupied a large subsided caldera formed from volcanic activity 2.76 million years ago (Aziz-Ur-Rhamen & McDougal, 1972). Sediments from the surrounding Portland Limestone were levelled and redeposited as sedimentary beds within the 'Nelson Bay caldera lake' (White, 2002). These sediments in turn formed calcarenite beds, interspersed with clay beds. The clay beds in the caldera lake sediments are marked by the presence of rip-up clasts formed by strong currents during periods of flooding of the lake, and form a portion of the Nelson Bay Formation.

The Nelson Bay Formation includes a distinct unconformity, forming a boundary between the Upper Nelson Bay Formation and the Lower Nelson Bay Formation. This unconformity has been correlated with the Gunz Glacial Peak (Boutakoff, 1963), implying a minimum age of 0.73my for the underlying Lower Nelson Bay Formation. The sediments of the Lower Nelson Bay Formation have been described as approximately 10m of clay beds, which includes approximately 3m of horizontally bedded calcarenite, resting on 2m of sandy clay. This in turn rests upon pink sandy clay soils (Boutakoff, 1963). It is the sandy clay soils that form the fossil bone beds in the Lower Nelson Bay Formation. The presence of the formaminiferal species *Globoratalia truncatulinoides* in the sediments of the Nelson Bay Formation implies a maximum age of 1.9my for this unit (Srinivasan & Kennet, 1981). Magnetic polarity stratigraphy studies have concluded that the Nelson Bay Formation represents an age of 1.63 – 0.71 my (Whitelaw, 1991). MacFadden (1987) noted that the Nelson Bay Formation is significant in terms of palaeontological, radio isotopic and palaeomagnetic data leading to a relatively precise geochronology for the formation (MacFadden et al 1987). Kenley assigned the Nelson Bay Formation to the Early Pleistocene (Kenley 1988, p. 366). Rich et al. (1991) also stressed that the Nelson Bay Local Fauna "is the single securely dated Early Pleistocene assemblage from either Australia or Papua New Guinea."(p. 1014). White (2002) noted that five distinct fossil bone beds are present in the Lower Nelson Bay Formation. The collection of the material described here can not be located precisely to a particular bone bed described, but it originated from the Lower Nelson Bay Formation approximately 50m west of the sewer outfall, and was at the time of collection approximately 1.5m above the beach sand in front of the cliff. The material can therefore be considered Early Pleistocene in age.

The Nelson Bay Local Fauna

Hann (1983) partially described the 'Nelson Bay Local Fauna' in an unpublished Honours thesis, which was subsequently updated by Herrmann (2000) in an unpublished Masters thesis. Whitelaw (1991) referred to the Nelson Bay Local Fauna in terms of geochronology, however the composition of this Local Fauna was not included in this reference. White (2002) compiled a list of identified fossil species from this

locality which comprise the fauna identified prior to 2000 and included additional material in the local fauna which was identified for the purposes of that study. A combined lists of species from the Nelson Bay Local Fauna is provided in Table 2.

SYSTEMATIC PALAEONTOLOGY

Subclass MARSUPIALIA Illiger, 1811

Cohort AUSTRALIDELPHIA Szalay, 1982

Order DASYUROMORPHIA Gill, 1872

Superfamily DASYUROIDEA Goldfuss, 1820

Family DASYURIDAE Goldfuss, 1820

Genus *Sarcophilus* Geoffroy Saint-Hilaire & Cuvier, 1837

Type Species *Sarcophilus laniarius* (Owen, 1838)

Selected synonymy.
Didelphis ursina Harris 1808: 176, pl. 19.
Dasyurus laniarius Owen 1838: 369, pl. 49, figs 3-7.
Sarcophilus harrisii Boitard 1842: 290, Merigian *et al.* 2002: 84, fig. 2C, fig 8A-F.
Sarcophilus (Dasyurus) ursinus Owen, 1877: 105, pl. 13, figs 2, pl. 15, fig 2.
Sarcophilus (Dasyurus) laniarius Owen, 1877: 105, pl. 5, figs 1-6, pl. 14, fig 2.
Sarcophilus satanicus Thomas, 1903: 289.
Sarcophilus laniarius laniarius Owen, 1838, - Werderlin, 1987: 9.
Sarcophilus laniarius Owen, 1838, Long *et al.* 2002: 55.

Description of material. The illustrated material collected at Nelson Bay comprises a complete lower molar series (M/1, M/2, M/3 and M/4), a single lower premolar (P/2), and canine. The material is composed of teeth only, traces of mandibular material were found associated with the suite of teeth but disintegrated on collection. There is no doubt that all the teeth derived from a solitary individual. The canine is crescentic, denuded of dental enamel and shares the robust morphology of the *S. laniarius harrisii* used for

Fig. 1. Sarcophilus laniarius harrisii, labial view. Scale bar intervals represent 10mm.

comparative purposes. The premolar (P/2) is composed of enamel and a single root consistent with *S. laniarius harrisii* morphology. M/1, M/2 and M/3 are complete teeth with enamel and roots intact, M/1 showing a degree of occlusal wear consistent with mature sarcophiloid dasyurids. M/4 is fragmentary (in two portions) with much of the talonid missing, break is a vertical 'crack' from protoconid. Trigonid of M4/ present, talonid is absent.

A list of 22 morphometric characteristics of the lower dentition of *S. laniarius harrisii* were recorded from 20 individuals. This morphometric data was then compared to corresponding characteristics on the Nelson Bay material, and is shown in Table 3. The Nelson Bay material is unquestionably from *S. laniarius harrisii* on the basis of this comparison.

Sarcophilus laniarius harrisii Boitard, 1842

Discussion. Considerable discussion on the dental morphology and fossil record of *S. laniarius harrisii* is available. Archer (1976) discussed dasyurid dental nomenclature and demonstrated the relationships of dasyurids (including *S. harrisii*) to didelphids, thylacinids, borhyaenids and peremelids. Archer (1982) reviewed the dasyurid fossil record (including *S. harrisii*), and investigated the phylogeny of dasyurids generally. Wroe *et al.* (2000) investigated the dental and cranial characteristics of dasyurids (including *S. [laniarius] harrisii*) using cladistic analysis for phylogenetic analysis. The dental morphological characteristics assigned to *S. laniarius harrisii* in these investigations conform closely to the Nelson Bay material. The illustrated specimen was also compared with the holotype *of S. moornaensis* and was shown to share broad morphological affinities consistent with the generic distinction of *Sarcophilus*, but was found to differ in a combination of features, such as the generally smaller size of *S. moornaensis*. The *S. moornaensis* specimens also displayed more elongate M/3 and M/4 talonids, more distinct talonid cusps, better developed metaconids and more laterally compressed trigonids than the material described herein. Both the comparative *S. laniarius harrisii* material and Nelson Bay specimens have weaker metaconids than *S. moornaensis* and are larger than *S. moornaensis*. The new teeth are therefore assigned

Fig. 2. *Sarcophilus laniarius harrisii*, lingual view. Scale bar intervals represent 10mm.

to *S. laniarius harrisii* on the basis of close affinities to the comparative material.

Long et al. (2002), Gill (1953) and Archer *et. al.*, (1984) considered the time range of *Sarcophilus* to be early Pleistocene to present day, noting the occurrence of *S. laniarius harrisii* in many Pleistocene faunas throughout mainland Australia and Tasmania. Dawson (1982), in reviewing the taxonomic status of specimens from eastern Australian fossil localities, included *S. laniarius* fossil material no older than 30,000 years old, and considered the time range of *S. laniarius* to be Pleistocene. Guiler (1982) discussed the temporal distribution of *S. laniarius harrisii* on mainland Australia, citing fossil material no older than 5000 years old. Due to the geochronology of the bone beds in the Lower Nelson Bay Formation, the Nelson Bay material constitutes the geologically earliest recorded occurrence of verifiable age of *S. laniarius harrisii*.

The presence of *S. laniarius harrisii* in earliest Pleistocene sediments provides further information on the evolution of the sarcophilines. Archer and Bartholomai (1978, p. 5) recognized "A structural lineage starting with a hypothetical fossil form similar to *Dasyurus maculatus* Kerr, 1792, to *Glaucodon ballaratensis* Stirton, 1957, to the annectant extinct species of *Sarcophilus* and ending with *S. harrisii* is one of the best documented marsupial structural phylogenies", where the annectant species mentioned is *S. moornaensis*. *S. moornaensis* is considered early Pleistocene in age (Long et. al. 2002). The geochronology of the sediments containing the illustrated material implies *S. laniarius harrisii* may have existed contemporaneously with *S. moornaensis*, and as such *S. moornaensis* is not considered ancestral to *S. laniarius harrisii*. *Glaucodon ballaratensis* represents a sister taxon relationship to *Sarcophilus* and *Dasyurus*. Elsewhere in this issue the morphological similarities of *G. ballaratensis* to *Dasyurus maculatus* are discussed. The age of the illustrated material implies that the genus *Sarcophilus* arose at some point prior to the early Pleistocene from an ancestral form morphologically similar to *G. ballaratensis*. Future discoveries of Cenozoic and Quaternary sarcophiline material will provide further insight to the evolution of *Sarcophilus* and the placement of *Sarcophilus* in dasyurid phylogeny.

The new material in the Lower Nelson Bay Formation also provides additional information on the composition of the Nelson Bay Local Fauna and the implied environmental conditions of Nelson Bay in the early Pleistocene. Notably, the Nelson Bay Local Fauna is composed of an extensive and diverse list of macropodids of both the browsing and grazing dental grades. The presence of these forms implies a combination of palaeoenvironments may have surrounded the Nelson Bay Caldera Lake during the Pleistocene. The inclusion of arboreal forms such as the pseudocheirids suggest a forested environment may have existed close to the site of deposition, however the presence of grazing forms such as *Macropus* suggest grassland environments may have also been nearby.

Hann (1983) described the Nelson Bay Local Fauna as a biocoenosis in composition, implying the fauna once lived together prior to death and subsequent fossilisation. The Nelson Bay Local Fauna was also regarded as being derived from catastrophic mortality due to the presence of juveniles, young adults and mature adults (Hann, 1983). The

Location	**Age (in years)**	**Reference**
Strathdownie, Victoria	"Late Pliestocene"	Werderlin, 1987
Devil's Lair Cave, Western Australia	35,200 +/- 1,800	Archer, 1982
Keilor, Victoria	>18,000	Marshall, 1974
Buchan, Victoria	22,980 +/- 2,000	Flood, 1973
Lancefield, Victoria	26,000 +/- 500	Gillespie *et al*., 1978
Laura, Queensland	10,000 app.	Horton, 1977
Lake Menindee, New South Wales	18 - 26,000	Tedford, 1967
Laker Garnpung, New South Wales	>12,000	Hope, 1978
Dempsey's Lake, South Australia	>30,000	Wells, 1978
Kangaroo Island, South Australia	16,000 +/- 100	Hope et al., 1977
Queenscliff, Victoria	<10,000	Bartholomai & Marshall, 1972
Gisborne Cave, Victoria	<10,000	Gill, 1964

Table 1. Geochronologically dated fossil *S. laniarius* material from the Pleistocene and Holocene of mainland Australia

Subclass	Order	Family	Genus and species
Prototheria	Monotremata	Tachyglossidae	*Zaglossus robusta*
Metatheria	Polyprotodontia	Thylacinidae	*Thylacinus cynocephalus*
		Dasyuridae	*Sarcophilus* c.f. *laniarius harrisii*
	Diprotodonta	Thylacoleonidae	*Thylacoleo* sp.
		Ektopodontidae	*Darcius 'braileyi'*
		Pseudocheiridae	*Pseudocheirus* c.f. *peregrinus*
			Pseudocheirus c.f. *stirtoni*
			Giant *Pseudocheirus* sp.'
		Diprotodontidae	*Diprotodon* c.f. *optatum*
			Zygomaturus trilobus
		Palorchestidae	*Palorchestes* c.f. *parvus*
		Macropodidae	*Sthenurus* sp.
			Protemnodon brehus
			Protemnodon anak
			Macropus sp.
			Macropus c.f. *titan*
			Baringa nelsonensis
			Thylogale c.f. *billardierii*
			Thylogale sp.
			Lagostrophus sp.
			Onychogalea sp.
			Setonix brachyurus
			'Very small macropodid'
		Potoroidae	indet.
Eutheria	Rodentia	Muridae	*Pseudomys* c.f. *shortridgei*

Table 2. The Nelson Bay Local Fauna, adapted from White (2002) and Herrmann (2000).

CHARACTER	***Sarcophilus harrisi*** (n) = 20	***Sarcophilus moornaensis*** (n) = 1	**Portland *Sarcophilus*** (n) = 1
M1 length	9.2	7.8	9.2
M1 width	6.2	5.2	7
M1 trigonid length	7	7.2	4.3
M1 trigonid width	4.5	5	6.4
M1 talonid width	4.9	3.2	5.9
M2 length	10.9	9.5	10.9
M2 width	6.5	5.9	8
M2 trigonid length	8.4	8.7	6.6
M2 trigonid width	5.2	3.8	5.9
M2 talonid width	3.3	4.5	4.9
M3 length	12	10	14.8
M3 width	7.4	6.3	8.7
M3 trigonid length	7.7	8	9.2
M3 trigonid width	5.6	5.4	6.6
M3 talonid width	2.3	3.3	4
M4 length	11.9	11.2	absent
M4 width	6.5	6.5	7.1
M4 trigonid length	9.9	10.2	>9.4
M4 trigonid width	4.8	4.6	>6.2
M4 talonid width	2.3	2.9	absent
P3 length	6	absent	>6
P3 width	6.7	absent	>4.4

Table 3. Comparative dental measurements of the Portland *Sarcophilus laniarius harrisii*

disconformities which truncate the bone beds in the Lower Nelson Bay Formation were correlated with periods of substantial climatic change, which may have triggered the catastrophic mortality observed by Hann (White, 2002). The disconformities represent cool, dry climates which led to the accumulation of bone material on the land surface. Subsequent flooding at the beginning of the next warm, wet phase concentrated this bone material as basal lag deposits (White, 2002). Future investigations and discoveries from the Nelson Bay Local Fauna will provide a greater insight to the nature of early Pleistocene mammalian assemblages and environmental conditions on mainland south eastern Australia.

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SCOLOPENDRID CENTIPEDES CAUGHT BY PITFALL TRAPPING IN THE ULUṞU-KATA TJUṮA NATIONAL PARK, NORTHERN TERRITORY, INCLUDING A RECORD OF AN APPARENT 'OUTBREAK'

ALAN L. YEN[1,2] & JOHN WAINER[1,3]

[1]Museum Victoria, GPO Box 666E, Melbourne, Victoria 3001, Australia
[2]Present address: Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, PO Box 137, Heidelberg, Victoria 3084, Australia
[3]Present address: Institute for Horticultural Development, Department of Primary Industry, Knoxfield, PrivateBag 15, Ferntree Gully Delivery Centre, Victoria, 3156, Australia.

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Pitfall trap surveys of fauna were conducted in the Uluṟu-Kata Tjuṯa National Park in 1995, 1997 and 2000. Relatively low numbers of scolopendrid centipedes were trapped during most of the surveys, but heavy summer rainfall in early 2000 may have been responsible for large numbers of individuals trapped then. The surveys have recorded a total of six species of scolopendrid centipedes from the Park, bringing the total known species there to seven.

Key words: Scolopendrid centipedes, Uluṟu-Kata Tjuṯa National Park

AUSTRALIAN centipedes are classified into five orders: the Scolopendrida, Geophilida, Lithobiida, Craterostigmatida and Scutigerida (Harvey & Yen 1989). Scolopendrid centipedes are common in the drier regions of Australia. Fortyfour named species of scolopendrid centipedes are known from Australia, and they are predominantly solitary nocturnal predators (Edgecombe 2001) feeding on other invertebrates or occasionally on small vertebrates.

Recent faunal studies of both vertebrates and invertebrates in the Uluṟu-Kata Tjuṯa National Park have, under the joint management arrangement at the Park, involved participation by traditional owners (Aṉangu).

On the morning of 22 February 2000, drift fence pitfall traps that were running as part of a spinifex fire age faunal survey in the Uluṟu-Kata Tjuṯa National Park caught enormous numbers of scolopendrid centipedes – a total of 945 individuals in 54 traps (an average of 17.5 centipedes/trap)! The Uluṟu fauna surveys, conducted in 1995, 1997 and in October 2000, using the same trapping techniques but at different locations within the Park, found relatively small numbers of centipedes. This apparent 'outbreak' in numbers of centipedes was common knowledge amongst the Aṉangu, who recognise several different colour forms, and had also been reported at the nearby tourist resort at Yulara. However, it had not been recorded in the scientific literature, and this was an opportunity to determine which species of scolopendrid centipedes occurred in the area, and whether particular species had these apparent spectacular increases in numbers.

In this paper we enumerate the scolopendrid centipedes trapped during the spinifex fire age faunal survey in February-March 2000 (SFS) in relation to sites and dates, and will compare results with the three Uluṟu fauna surveys (UFS) in 1995, 1997 and October 2000.

METHODS

The Uluṟu fauna surveys were conducted in March-April 1995, September-October 1997 and October 2000. The fauna surveys involved eight sites (Fig. 1), and the same eight sites were sampled in 1995, 1997 and 2000 (Yen *et al.* 1996): UFS 1 (Open grassland to woodland at the base of Uluṟu), UFS 4 (Mulga shrubland), UFS 5 (Soft spinifex), UFS 6 (Hard spinifex), UFS 7 (Mallee shrubland), UFS 8 (Sandhill mulga), UFS14 (Hard spinifex transitional sandplain), and UFS15 (Alluvial fans and watercourse, Shrubland

to River Red Gum creekbed adjacent to Kata-Tjuṯa). The 2000 spinifex fire-age survey involved six sites (sites 1-6), each of which was divided into three classes of spinifex (older spinifex, younger spinifex, and ecotone). There were two replicates of each spinifex class at each site, resulting in six trap lines within each site. The term "spinifex" is used in this report to describe the various species of hummock grasses found in the study areas. The older spinifex sites (labeled A and B) were last burnt in 1976 or earlier. The younger spinifex sites (E and F) were burnt more recently. In all cases, there was an ecotone between the older and younger spinifex (labeled C and D). The SFS sites are shown in Fig. 1, and the dates on which the pitfall traps were run in 2000 were: SFS 5 (17-20 Feb), SFS 3 (21-24 Feb), SFS 2 (24-27 Feb), SFS 1 (27 Feb – 01 Mar), SFS 4 (01-04 Mar) and SFS 6 (04-07 Mar).

Centipedes were collected by drift fence pitfall trapping. At each site, the pitfall traps were arranged along two intersecting 25 metre lines arranged at right angles to each other, thus forming a cross. The traps were 20 litre buckets. One bucket was located at the intersection of the lines and four additional buckets along each line at six metre intervals. Consequently each pitfall trap site consisted of a set of nine buckets. A nylon drift fence was run along each line to connect the buckets. Within each sampling site, several replicate pitfall lines were operated concurrently. In both the UFSs and the SFS, the same pitfall trap line configuration was used; the only difference was that in the UFS, there were 4 sets of pitfall traps at each site, while in the SFS, there were 6 sets of pitfall traps. The traps were opened for three nights at each site, and examined in the morning and the evening. All invertebrates in the pitfall traps were collected with forceps and preserved in 70% ethanol. All pitfall trap material was eventually identified to the morphospecies level and lodged in the Museum of Victoria.

No attempt will be made in this paper to determine what environmental factors may be important in determining scolopendrid distribution in the UFS and the SFS sites. In the UFS, scolopendrid numbers, both in terms of species and individuals, are in the main low. Superficially, there did not seem to be a consistent trend of scolopendrid association with any of the major plant communities in the UFS. In the SFS, replicates were taken in older and younger spinifex, and ecotones, and the numbers of scolopendrids in these different aged spinifex is considered.

RESULTS

The predominant family of centipedes collected in the pitfall traps was the Scolopendridae. A very small number of centipedes belonging to the Scutigeridae were collected, but they have not been included in this paper. This dominance of the centipede fauna by the Scolopendridae was also found in the Carnarvon Basin of Western Australia (Harvey *et al.* 2000). Unless otherwise stated, results from the UFS and the SFS are presented as number of individuals collected in each site, combining data from each of the pitfall lines. Consequently data from the UFS are based on 4 pitfall lines, while data from the SFS are based on 6 pitfall lines.

Fauna surveys 1995, 1997 and 2000

The numbers of scolopendrids trapped was low in all three surveys (Table 1). Except for two occasions, fewer than 10 individuals were caught in any one pitline in any year. The exceptions were in 1995, when 24 *Ethmostigmus curtipes* were caught in pitline 3 at Site 15 and 20 *E. curtipes* in pitline 4 at Site 15. There was light rain on the night before these were trapped. While these two pitlines were adjacent, they were very different in vegetation: P3 was located in Ti-tree on sand and P4 on River Red Gum creek bed (primarily sand and rock).

In 1995, four species of scolopendrids were trapped, comprising a total of 121 individuals. They were dominated by two species: *Ethmostigmus curtipes* (67.8%) and *Scolopendra morsitans* (27.3%) (Table 1). In 1997, five species (84 individuals) were trapped. *E. curtipes* was again the dominant species, but much reduced in proportion (32.1%); *Scolopendra morsitans* (31.0%) was similar to 1995, while *Cormocephalus* sp. 2 (15.5%), *Cormocephalus* sp. 1 and *E. pachysoma* (10.7% each) occurred in higher proportions (Table 1). In the 2000 UFS, six species (69 individuals) were collected. The percentage compositions were similar to 1997 except that *E. pachysoma* was much reduced: *E. curtipes* (33.3%), *Scolopendra morsitans* (31.9%), *Cormocephalus* sp. 2 (15.9%) and *Cormocephalus* sp. 1 (14.5%) (Table 1).

The occurrence of each of the scolopendrid species thus varied in abundance and distribution over time and space. *Scolopendra morsitans* comprised approximately 33% of the individuals collected in each of the three faunal surveys; it occurred at all eight sites every survey with the exception of UFS 7 in 2000.

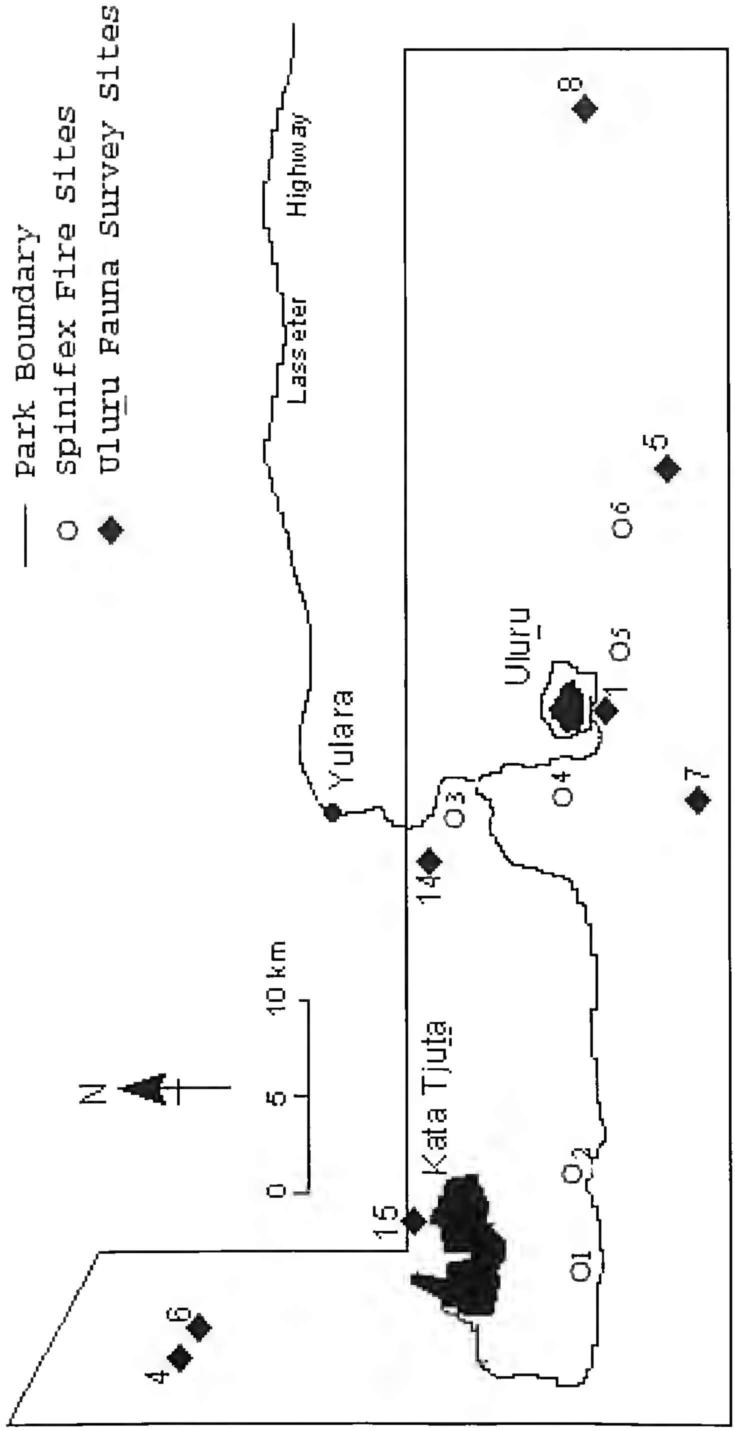

Fig. 1. Map of Uluru-Kata Tjuta National Park showing location of sites

Cormocephalus sp. 1 and 2 were either absent or very low in numbers in 1995, and comprised 10-15% of individuals collected in 1997 and 2000; over the 3 surveys, both species occurred in a total of five out of the eight UFS sites. *E. curtipes* ranged from 33-66% of the individuals trapped, and over the three surveys, was found in all eight UFS sites. In contrast, *E. pachysoma* and *E. rubripes* occurred in low numbers throughout the surveys and were only trapped in 3 of the UFS sites (Table 1).

The number of species trapped at any one site varied from one to five depending upon the year (Table 1). It is worth noting that over the three surveys, all six species were trapped in two sites (UFS7 and UFS8), five species at UFS5, four at UFS15, while only two species were trapped at UFS2 and three species at UFS1, UFS6 and UFS14 (Table 1).

Spinifex fire survey 2000

A total of 6 scolopendrid species, comprising 1859 individuals, was collected (Table 2). The fauna, based on percentage composition, was dominated by *E. pachysoma* (53.7%), *E. curtipes* (33.8%) and *Scolopendra morsitans* (11%). These three species were trapped at all six SFS sites, although their abundances, except for *Scolopendra morsitans*, varied between sites. *E. rubripes* was trapped in four of the SFS sites, while *Cormocephalus* sp. 1 and sp. 2 were trapped in three and two sites respectively (Table 2). In terms of relative abundances, *E. curtipes* dominated at four of the six SFS sites (SFS 1, 4, 5 and 6), *E. pachysoma* dominated at SFS3 and *Scolopendra morsitans* dominated at SFS5.

The sudden enormous increase in scolopendrid numbers caught in pitfall traps occurred at SFS3. Pitfall traps were opened at this site on the morning of 21 Feb and closed on the morning of 24 Feb. There was heavy rain on 19 Feb (36.5 mm) and 20 Feb (66.2 mm) before the traps at SFS3 were run (traps were SFS5 were open during the heavy rain). The pitfall traps had large numbers of centipedes on the morning of 22 Feb, followed by fewer on the mornings of Feb 23 and 24. The pitfall trap samples on the morning of 22 February were kept separate from those of the mornings of 23-24 February (when there were fewer centipedes). The data from SFS3 are presented in Table 3. The catch on 22 February was primarily *Ethmostigmus pachysoma*, between 124-180 individuals at each of the six pitfall lines. Small numbers of *E. curtipes* and *Scolopendra morsitans* were trapped on 22 February. The number of *E. curtipes* caught in the traps was larger on 23-24 February, although the number of *E. pachysoma* trapped was marginally higher in three trap lines on these dates. In general, the major occurrence was the enormous increase in *E. pachysoma* numbers on the night of 21 February (and possibly very early in the morning of 22 February), and a sudden drop, although not a disappearance, on the nights of 22 and 23 February.

The SFS was conducted over 20 consecutive days. Considerable rainfall occurred on several days preceding the survey and also during the survey, and it is possible that this rain influenced centipede activity. The abundances of each species of centipede at each of the sites during the SFS are plotted in Fig. 2. *Scolopendra morsitans* was relatively steady in numbers at all sites during the SFS. *Cormocephalus* sp. 1 and sp. 2 occurred in low numbers after Feb 24. The responses of the three *Ethmostigmus* species differed; *E. curtipes* occurred in relatively high numbers throughout the survey, *E. pachysoma* occurred in very high numbers earlier during the survey, while *E. rubripes* occurred in relatively low numbers in four of the six sampling occasions.

The scolopendrid distribution between the different aged spinifex sites is presented in Table 4. More scolopendrids were trapped in older spinifex (A+B), followed by ecotones (C+D) and lowest numbers in younger spinifex (E+F). When examined on a species basis, the major differences in the different spinifex types is due to *Ethmostigmus curtipes*, which seems to prefer older spinifex over younger spinifex (Table 4).

DISCUSSION

There are few previous records of scolopendrid centipedes from the Uluru-Kata Tjuta National Park. In his revisions of Australian scolopendrids, Koch noted three species from within the Park: *Scolopendra laeta* Haase from Mt Olga and west gorges of Mt Olga (Koch 1982), *Scolopendra morsitans* L. from Mt Olga (Koch 1983a) and *Ethmostigmus rubripes* (Brandt) from Ayers Rock (Koch 1983b). The UFS and the SFS added a further four species of scolopendrid, taking the number of recorded species to seven. Harvey *et al.* (2000) collected 13 species of scolopendrid centipedes by pitfall traps in the Carnarvon Basin of Western Australia, although their study was conducted over a wider geographical region and they ran pitfall traps continuously over a 12 month period.

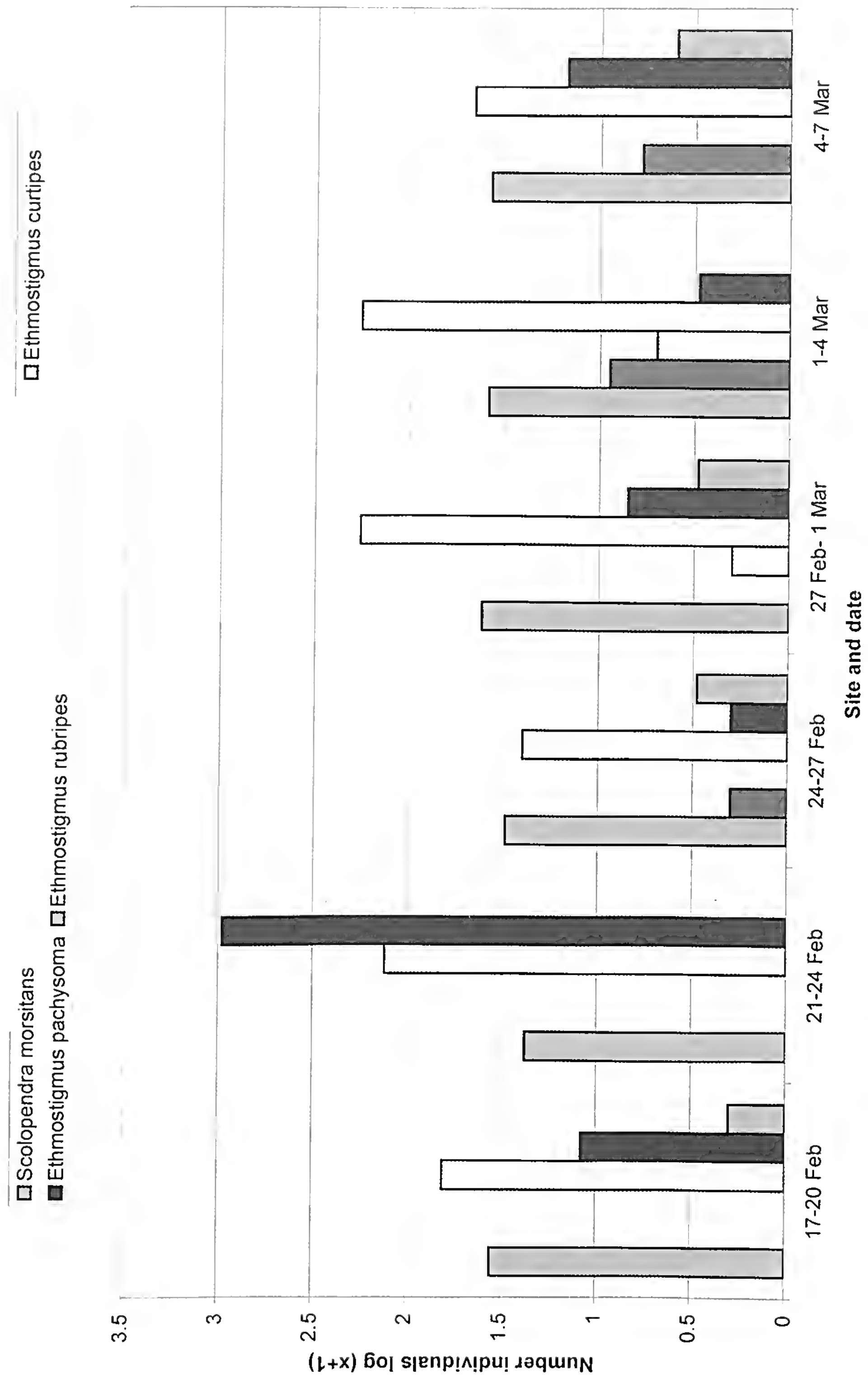

Fig. 2. Centipedes from spinifex fire survey

There are three issues to be discussed with regard to the scolopendrids trapped in the surveys at Uluru-Kata Tjuta. They are (1) the numbers of individuals collected by pitfall trap studies; (2) the response of the scolopendrids to heavy rain; and (3) the role of scolopendrids in the arid systems of Central Australia.

Numbers of individuals and pitfall trapping

In the few published studies on population densities of centipedes, the densities are generally low. The only scolopendrid species studied with regard to density are *Scolopendra amazonica* in Nigeria, which has a density of $0.16/m^2$ (and a biomass of 140 mg/m^2), although pitfall trapping was not the collecting method employed (Lewis 1972a). While it is difficult to estimate densities from pitfall trap studies, they can give an indication of whether numbers are low or high. In a fauna survey of the Mallee in north-western Victoria, drift fence pitfall trapping collected centipedes (Robertson *et al.* 1986), and a total of 1026 specimens, comprising 14 species, was collected (Yen & Lillywhite, unpublished data). However, the traps were spread over 122 sites, and each site comprised 10 x 20 litre pitfall traps which were run for five nights on five occasions over an 18 month period, giving an average of less than 2 individuals per pitfall line on each collecting occasion. Corey (1988) used pitfall traps in three plant communities over a six month period (detailed pitfall trap methodology were not given) in Florida (USA), and collected only 28 individuals from 5 species.

Throughout the UFS, the number of scolopendrid centipedes collected in pitfall traps was relatively low. The very large numbers were found at different sites during the SFS during a time of heavy summer rain. However, it appears that during the periods of no or minor rainfall, scolopendrid activity, and consequently catches in pitfall traps are low. The trap records from the Uluru fauna surveys suggest that the densities of scolopendrid centipedes are low.

Response of centipedes to heavy rain

However, the large numbers collected during the SFS suggest that scolopendrid densities may not be as low as suggested by results from the UFS. It is difficult to make definitive conclusions about this because (1) the SFS sites did not coincide with the UFS sites; and (2) it is not possible to distinguish site-specific differences or the effects of heavy rain at the SFS sites because the pitfall traps at each site were run sequentially over time.

In Nigeria, the beginning of the rainy season initiated dispersal of young centipedes (Lewis 1972b). In South-East Asia, responses of two species of scolopendrid centipedes to water differed: *Scolopendra subspinipes* swims when immersed, while *Arrhabdotus octosulcatus* cannot swim and walks under water with its head out of the water. The latter is probably an arboreal species while the former is more likely to experience flooding from tropical down pours (Lewis 1980). Finally, flushing with water has been used as a collecting technique for centipedes (Lewis 1972a).

The results suggest that the increased activity of centipedes, and consequently the larger total numbers trapped, during the SFS is due to heavy rainfall. However, the responses seem to be related to the individual species, especially *Ethmostigmus pachysoma*. The numbers of *Scolopendra morsitans* and *Ethmostigmus curtipes* were steady throughout the SFS, while the numbers of both *Cormocephalus* species and *Ethmostigmus rubripes* remained relatively low. It is suggested that the generally higher rainfall may be responsible for the increased numbers of centipedes caught in the pitfall traps, but the rain may have affected some species more than others. The large numbers of *E. pachysoma* occurred on Feb 21-24 at site SFS3, when the numbers of *Scolopendra morsitans* was lowest and no *Cormocephalus* species or *Ethmostigmus rubripes* were trapped. This may indicate that the last three species did not occur at SFS3, that *E. pachysoma* and *E. curtipes* have higher densities at this site, and the recorded response was due to the heavy rain in the days preceding the trapping. There was even heavier rainfall on 11-13 February, before the SFS began, and it is possible that any response to heavy rain by centipedes may be rapid and short.

Anecdotal information from traditional owners and from visitors to the area indicate previous increased centipede activity after heavy rains. Whether the response is a cue for some aspect of centipede behaviour (dispersal, mate seeking, etc) is not known, although most individuals collected seemed to be mature. Alternatively, the increased activity may simply have been due to centipedes being flushed out of their subterranean habitat.

1995 Uluru fauna survey	S1	S4	S5	S6	S7	S8	S14	S15	Total	%
Scolopendra morsitans	4	2	11	2	1	7	4	2	33	27.3
Cormocephalus sp. 1	0	0	4	0	0	0	0	0	4	3.3
Cormocephalus sp. 2	0	0	0	0	0	0	0	0	0	0
Ethmostigmus curtipes	6	5	1	0	0	4	0	66	82	67.8
Ethmostigmus pachysoma	0	0	0	0	0	0	0	0	0	0
Ethmostigmus rubripes	0	0	0	0	1	1	0	0	2	1.7
Total number individuals	10	7	16	2	2	12	4	68	121	
Number species	2	2	3	1	2	3	1	2	4	

1997 Uluru fauna survey	S1	S4	S5	S6	S7	S8	S14	S15	Total	%
Scolopendra morsitans	2	2	6	5	2	2	4	3	26	31
Cormocephalus sp. 1	3	0	4	0	0	0	0	2	9	10.7
Cormocephalus sp. 2	0	0	0	7	1	0	5	0	13	15.5
Ethmostigmus curtipes	4	0	8	3	0	7	5	0	27	32.1
Ethmostigmus pachysoma	0	0	1	0	3	5	0	0	9	10.7
Ethmostigmus rubripes	0	0	0	0	0	0	0	0	0	0
Total number individuals	9	2	19	15	6	14	14	5	84	
Number species	3	1	4	3	3	3	3	2	5	

2000 Uluru fauna survey	S1	S4	S5	S6	S7	S8	S14	S15	Total	%
Scolopendra morsitans	3	3	5	2	0	3	3	3	22	31.9
Cormocephalus sp. 1	1	0	2	0	4	1	0	2	10	14.5
Cormocephalus sp. 2	0	0	3	0	1	2	5	0	11	15.9
Ethmostigmus curtipes	4	0	0	1	3	4	4	7	23	33.3
Ethmostigmus pachysoma	0	0	1	0	0	0	0	0	1	1.4
Ethmostigmus rubripes	0	0	0	0	0	1	0	1	2	2.9
Total number individuals	8	3	11	3	8	11	12	13	69	
Number species	3	1	4	2	3	5	3	4	6	

Table 1. Number of species and individuals of scolopendrid centipedes trapped in the 1995, 1997 and 2000 Uluru fauna surveys

The role of scolopendrids in the arid systems of Central Australia

If we accept that centipede activity is low during times of non-rainfall or light rainfall, and that heavy rainfall flushes out large numbers, then the densities of scolopendrids living in the sand may be much higher than we imagine. Lewis (1981) reported that centipedes can survive aridity by burrowing deep into the soil. Anangu observed centipede burrows in the sand at Uluru. The question arises as to whether they form structured burrows or whether they simply 'swim' in sand. Other interesting topics include how frequently they emerge above ground, and whether they catch food in their subterranean habitat. *Scolopendra* and *Cormocephalus* are solitary species (Lewis 1981).

It is interesting to speculate upon the ecological role that centipedes play in the semi-arid and arid zones of Australia. Intraspecific encounters are usually aggressive (Edgecombe 2001). They are relatively large predators (in invertebrate terms), and as such would be expected to play a significant role in view of the large numbers trapped during the SFS. A wide variation in the diets of scolopendrids has been recorded from around the world; food ranges from invertebrates to small vertebrates (Lewis 1981). There is an abundance of potential invertebrate food for centipedes in Central Australia. The ground-active invertebrate fauna is dominated by ants and termites, and Anangu report that during dry conditions, centipedes catch ants as food. After rain, they emerge to catch termites. In turn, their relatively large body size would provide a decent meal for higher level predators, and Anangu report that they are eaten by sand goannas.

In the western desert region of Australia, centipedes are called 'wanatjiti' or 'kanparka' in the Pitjantjatjara language. According to the traditional owners (Anangu), there is Tjukurpa (Law) associated with centipedes; and some of this information is not available.

Much remains unknown about scolopendrid centipedes. Their basic life histories and longevity remains to be determined. Population numbers and fluctuations and habitat factors that influence their distribution are still unknown.

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We wish to thank Peter Lillywhite (Museum Victoria) and Greg Edgecombe (Australian Museum) for

	SFS1	SFS2	SFS3	SFS4	SFS5	SFS6	Total	%
Scolopendra morsitans	41	30	23	38	35	37	204	11
Cormocephalus sp. 1	0	1	0	8	0	5	14	0.8
Cormocephalus sp. 2	1	0	0	4	0	0	5	0.3
Ethmostigmus curtipes	183	24	131	181	64	46	629	33.8
Ethmostigmus pachysoma	6	1	965	2	11	14	999	53.7
Ethmostigmus rubripes	2	2	0	0	1	3	8	0.4
Total number individuals	233	58	1119	233	111	105	1859	
Number species	5	5	3	5	4	5	6	

Table 2. Number of species and individuals of scolopendrid centipedes trapped during spinifex fire age survey Feb-March 2000

assistance with identification of the centipedes, and Leigh Ahern for field assistance during the 2000 UFS. The work was conducted with financial support from Environment Australia, and we are indebted to Jake Gillen and Sam Rando for their organization of the project. Various staff members of Parks Australia North assisted with various aspects of these surveys, and traditional owners (Imantura, Daisey Walkabout, Joyce Tjalyiri, Ginger Tjintalka and Billywara) also provided support and information.

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	Site 3A		Site 3B		Site 3C		Site 3D		Site 3E		Site 3F	
	22-Feb	23/24 Feb	22-Feb	23/24 Feb	22-Feb	23/24 Feb	22-Feb	23/24 Feb	22-Feb	23/24 Feb	22-Feb	23/24 Feb
Scolopendra morsitans	1	0	2	5	3	1	2	1	1	1	3	3
Ethmostigmus curtipes	8	36	16	31	4	15	1	0	4	8	1	7
Ethmostigmus pachysoma	166	22	180	5	124	7	144	11	151	10	134	10

Table 3. Pitfall trap catches of scolopendrids at site 3 during 'outbreak' in February 2000. he traps were opened on 21 Feb and closed on 24 Feb.

SFS Site and date	Species	Old	Ecotone	Young
Site 1. 27 Feb - 01 Mar 2000	*Scolopendra morsitans*	13	20	8
	Cormocephalus sp. 1	0	0	0
	Cormocephalus sp. 2	1	0	0
	Ethmostigmus curtipes	92	72	19
	Ethmostigmus pachysoma	3	2	1
	Ethmostigmus rubripes	0	1	1
	Total	109	95	29
Site 2. 24-27 Feb 2000	*Scolopendra morsitans*	4	14	12
	Cormocephalus sp. 1	0	0	1
	Cormocephalus sp. 2	0	0	0
	Ethmostigmus curtipes	9	8	7
	Ethmostigmus pachysoma	0	0	1
	Ethmostigmus rubripes	0	1	1
	Total	13	23	22
Site 3. 21-24 Feb 2000	*Scolopendra morsitans*	8	7	8
	Cormocephalus sp. 1	0	0	0
	Cormocephalus sp. 2	0	0	0
	Ethmostigmus curtipes	91	20	20
	Ethmostigmus pachysoma	373	287	305
	Ethmostigmus rubripes	0	0	0
	Total	472	314	333
Site 4. 01-04 Mar 2000	*Scolopendra morsitans*	9	15	14
	Cormocephalus sp. 1	5	1	2
	Cormocephalus sp. 2	1	0	3
	Ethmostigmus curtipes	106	33	42
	Ethmostigmus pachysoma	1	0	1
	Ethmostigmus rubripes	0	0	0
	Total	122	49	62
Site 5. 17-20 Feb 2000	*Scolopendra morsitans*	16	10	9
	Cormocephalus sp. 1	0	0	0
	Cormocephalus sp. 2	0	0	0
	Ethmostigmus curtipes	13	45	6
	Ethmostigmus pachysoma	6	1	4
	Ethmostigmus rubripes	0	0	1
	Total	35	56	20
Site 6. 04-07 Mar 2000	*Scolopendra morsitans*	18	15	4
	Cormocephalus sp. 1	4	0	1
	Cormocephalus sp. 2	0	0	0
	Ethmostigmus curtipes	21	24	1
	Ethmostigmus pachysoma	2	9	3
	Ethmostigmus rubripes	0	1	2
	Total	45	49	11
	Total	45	49	11
Total for all sites	*Scolopendra morsitans*	68	81	55
	Cormocephalus sp. 1	9	1	4
	Cormocephalus sp. 2	2	0	4
	Ethmostigmus curtipes	332	202	95
	Ethmostigmus pachysoma	385	299	315
	Ethmostigmus rubripes	0	3	5
	Total	796	586	478

Table 4. Differences between old, ecotone and young spinifex sites

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THE BALLARAT METEORITE, A FOSSIL IAB IRON FROM VICTORIA, AUSTRALIA

WILLIAM D. BIRCH[1] & LEONARD E. SAMUELS[2]

[1]Museum Victoria, GPO Box 666E, Melbourne, Victoria, 3001, Australia
[2]Department of Materials Engineering, Monash University, Clayton, Victoria, 3168, Australia

BIRCH, W. D. & SAMUELS, L. E., 2003:11:30. The Ballarat meteorite, a fossil IAB iron from Victoria, Australia. *Proceedings of the Royal Society of Victoria* 115(2): 67-75. ISSN 0035-9211.

The Ballarat meteorite was discovered in a palaeoplacer ('deep lead') deposit during gold mining in the Park Company leases at Ballarat, Victoria, during the late 1860s to early 1870s. The meteorite is a 12–15g fragment from a type IAB iron that underwent disaggregation due to weathering and transport in a vigorous stream environment. The meteorite consists essentially of kamacite with a subgrain texture marked by partially resorbed Neuman bands and with plentiful schreibersite inclusions. The average nickel content is in the range 6.1–6.3 wt. % as determined by EPMA and INAA methods and with high Ge and Ga contents for the type. The maximum age of the meteorite is unconstrained but it is at least 3 million years old, as this is the age of the basalt flows that buried the palaeoplacer deposit immediately west of Ballarat. Reconstruction of the prebasaltic landscape indicates that the meteorite fell close to the drainage divide at the time and has probably not travelled far. The specimen has been preserved due to the reducing conditions maintained in the deep lead environment.

Key words: Ballarat, fossil meteorite, palaeoplacer, Victoria, IAB iron

THE BALLARAT meteorite is a new nickel-poor IAB iron found during 19th Century mining operations at Ballarat, Victoria, Australia. A single fragment, likely to have been about 15 g originally, was discovered in a buried palaeoplacer deposit in the Park Company gold mine between 1867 and 1874. The circumstances of its discovery are not known, but it appears to have found its way into the mineral collection of Henry Rosales (1820–1916), a Spanish-born, German-trained mining engineer, who was engaged in contract work in the region at the time. Rosales donated his mineral collection to the University of Melbourne in the 1890s. Many of his samples have original hand-written labels but, unfortunately, that for the meteorite fragment is missing. While its provenance may therefore be questioned, the overall documentation of the Rosales collection and the historical connections between Ballarat, Rosales and documented discoveries in the Park Company mine suggest the meteorite is authentic. The historical mineral collections of the University were transferred to Museum Victoria in the late 1980s and the meteorite was rediscovered some years later. At an unknown time, a small portion of the sample has been removed for analysis, which detected nickel. Whether this was done by Rosales at the Ballarat School of Mines laboratory is not known, but the sample was registered in the University collection as 'meteoric (sic) iron'. Following further investigation by the present authors, the Ballarat meteorite was approved by the Nomenclature Committee of the Meteoritical Society. It is catalogued as specimen E15649 in Museum Victoria's meteorite collection.

The discovery site

Rich shallow alluvial gold deposits were discovered in the Ballarat region in central Victoria in 1851. From the mid-1850s, mining began to follow the deposits deeper beneath younger sediments in the eastern part of the field and basalt flows to the west (Baragwanath 1923; Canavan 1988). Two major deep lead systems, the Inkerman and Golden Point leads, are buried by up to four lava flows of the Newer Volcanics, in places over 100 m thick in total (Fig. 1). Various companies took out leases and sank shafts to exploit the alluvial deposits. The Park Company was formed in November 1867 and by using several former companies'

shafts, opened up rich alluvial deposits in so-called "reef wash", at depths between about 250 and 320 feet (75–100 m). These were in an area between the Inkerman and Golden Point leads to the north and southeast, respectively, and about 30 metres above them (Baragwanath 1946). Until it closed in March 1874, the mine produced 95 000 ounces of gold.

Although the precise location within the Park Company mine is not known, the coordinates for the discovery site of the Ballarat meteorite would be close to 37· 34' 15" S; 143· 49' 55" E.

Several other metallic minerals were collected from the Park Company lead at about the same time. Rolled fragments of native copper and galena were recorded by Krausé (1882, 1896). Galena and pyrite specimens from the mine were exhibited in the Philadelphia Exhibition of 1875/6. While there is no specific mention of 'native iron' being found, it appears that some systematic collecting of unusual metallic minerals was undertaken while the mine was operating.

Features and composition of the meteorite

The surviving piece of the Ballarat meteorite is a rough flattened mass of about 10 g, with dimensions 20 x 15 x 5 mm (Fig. 2). A fragment of about 1.5 g was removed to prepare a polished section and one of about 0.25 g for instrumental neutron activation analysis (INAA). There is only a very thin rust coating on the bright metal, which shows no propensity to alter under ambient conditions. The hackly surface of the piece suggests it is a fragment broken from a larger crystalline mass of kamacite, probably during transport.

In polished section the texture shows subgrains of kamacite crossed by partly resorbed Neumann bands and with scattered roughly prismatic crystals of schreibersite ('rhabdite') up to about 0.05 mm long (Fig. 3). In detail these have ragged margins marked by an unknown precipitate (possibly carlsbergite or, less likely, roaldite) that appears to represent an incipient reaction halo with the enclosing kamacite (Fig. 4). These features closely resemble those of the rhabdites described from the Veevers IIAB iron by Bevan *et al.* (1995). Throughout the matrix kamacite and along the boundaries of Neumann bands are minute grains of another unknown phase. One outer portion of the fragment shows markedly deformed features, suggestive of a strong localised impact during transport. Rhabdite crystals have been bent along shear planes in the deformed section. The boundary between this deformed region and the main kamacite body is possibly a fragmented schreibersite grain (Fig. 5).

The meteorite was analysed for major elements (Fe, Ni, Co, P) using an electron microprobe and for Ni and minor elements by INAA. The average Ni content from 22 microprobe analyses is 6.1 wt % (range 5.6–6.6), slightly lower than the 6.3 wt % obtained by the INAA method (see Table 1). Ga, Ge and Ir contents of 95, 480 and 1.1 i g/g, respectively, indicate that Ballarat is a low Ni, high-Ga and high-Ge IAB iron, rather than a IIAB iron.

Analyses of seven schreibersite grains gave a formula of $Fe_{1.64}Ni_{1.36}P$.

GEOLOGICAL CONTROLS ON AGE AND PRESERVATION

The palaeoplacer in which the Ballarat meteorite was found forms part of an extensive Cainozoic fluvial system in the West Victorian Uplands, in which rivers flowed north and south from an E–W-trending divide (Canavan 1988). The oldest palaeoplacers are

	Fe wt%	Ni wt%	Co wt%	P wt%	Ga ?g/g	Ge ?g/g	Ir ?g/g
Microprobe	94.17	6.10	0.36	0.035			
INAA		6.3			95	480	1.1

Table 1: Chemical analyses of the Ballarat meteorite

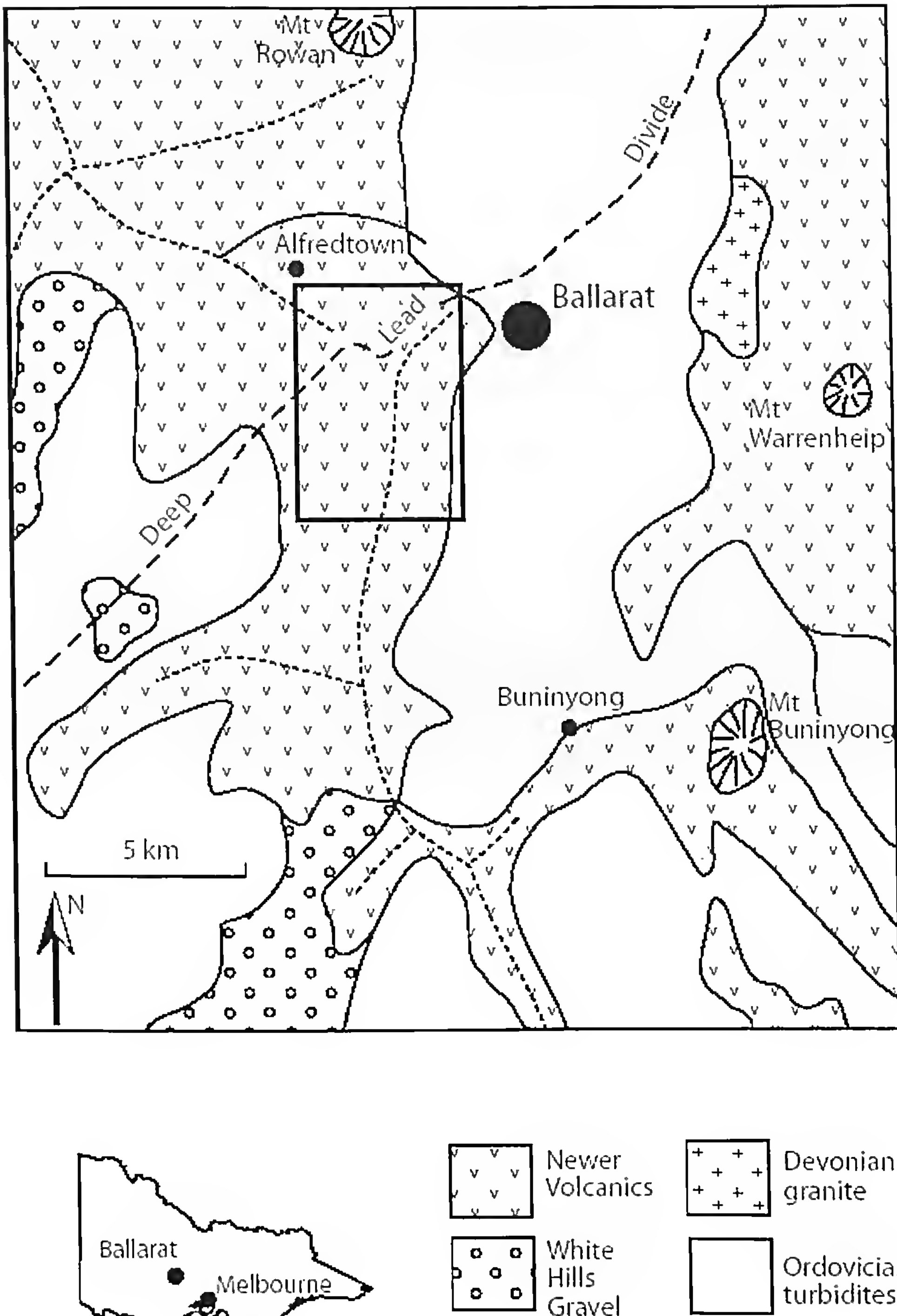


Fig. 1. Simplified geological map of the Ballarat district (after Finlay & Douglas, 1992). Main deep leads are shown as dotted lines. Lava flows from Mt Rowan eruption point cover the deep leads to the west of Ballarat, including the leases operated by the Park Company (see Fig. 6 for detail indicated by rectangle).

Fig. 2. The fragment of the Ballarat meteorite remaining after samples were removed for microscopy and analysis. The piece is 20 mm long. Museum Victoria specimen E15649.

unfossiliferous sheets of coarse quartz gravels known as the White Hills Gravel. These were laid down, probably in the very early Cainozoic, in broad shallow valleys cut into a landscape that had undergone extensive weathering. Later, younger, narrower valleys began to develop within the older broad valleys containing the White Hills Gravel. As this system advanced, streams eroded through the blanketing White Hills Gravel and incised valleys into the Palaeozoic bedrock, leaving remnant patches of gravel perched on interfluves. The conglomerates, sands, clays and lignites laid down in these new valleys were to become known as 'deep leads', which in many parts of the region were extremely rich in secondary gold. These palaeoplacers were deposited at different times and at different elevations, during cycles of downcutting and back-filling. Many were subsequently buried by Pliocene and younger basaltic lava flows. Lack of fossils, later faulting and inadequate outcrop mean that the palaeoplacers are difficult to date and correlate. Dating of rare pollen remains shows that some of these deep leads began to develop as early as the late Eocene. However, deposition was long-lived and continued right through until the Pliocene, when extensive volcanism caused disruption of the palaeodrainage systems (Hughes & Carey 2002).

In the Ballarat goldfield, there are several types of gold-bearing palaeoplacers. Baragwanath (1923) considered that pre-basaltic 'deep lead reef wash', such as was worked in the Park Company leases in the western part of the field, was probably equivalent to remnant patches of gravel outcropping on low hills to the east. These exposed patches are now regarded as the early Cainozoic White Hills Gravel (Taylor et al. 1996). Historical descriptions of the buried reef wash describe a similar lithology of well-water-worn pebbles and boulders of quartz, some of enormous size, with subordinate fragments of bedrock (slate and sandstone) and pieces of water-worn siliceous cemented material from older deposits. Typically, reef wash

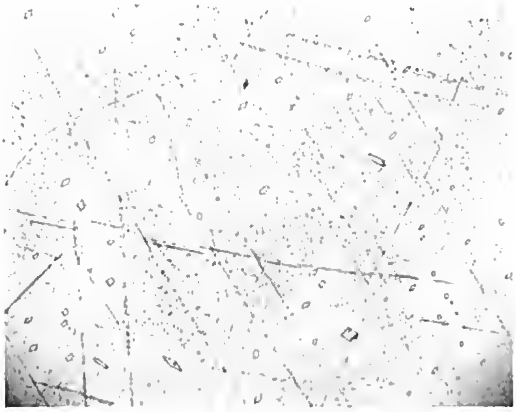


Fig. 3. General texture of the Ballarat meteorite showing subgrain boundaries in kamacite with partly resorbed Neumann bands and crystals of schreibersite. Field of view is about 1.5 mm across.

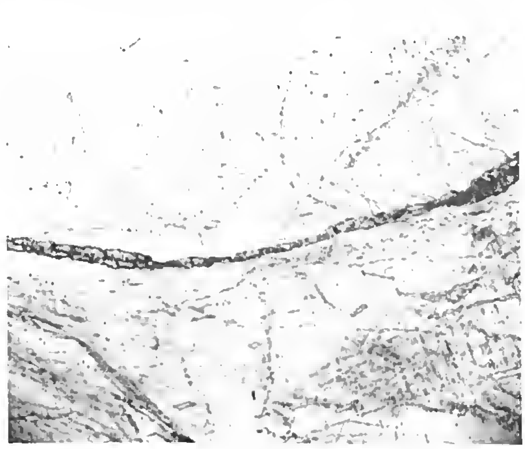
Fig. 4. Schreibersite prism showing incipient reaction halo with the enclosing kamacite. Field of view is about 0.08 mm across

deposits were spread over an expanse of flat or undulating bedrock above the normal level of the main stream channel or 'gutter' (Hunter, 1909). Channels up to 60 m deep were cut through the reef wash by later streams and filled with 'gutter wash' which, after burial by lava flows, form the deep leads proper.

The palaeodrainage system in the vicinity of the meteorite's discovery has been investigated by Taylor & Gentle (2002), using bore-hole data and mine records. A reconstruction of the prebasaltic bedrock topography suggests that a 'deep lead divide' separated the Inkerman and Golden Point leads. Trending generally NE–SW, the divide passed through the area mined by Park Company (Fig. 6). It appears that the reef wash the company removed came mainly from two poorly delineated remnants of an older fluvial system preserved on either side, but close to the top, of the divide.

This geological environment provides some constraints on the timing and location of the fall of the Ballarat meteorite. Based on the reconstruction of Taylor & Gentle (2002), the divide on which the meteorite-bearing gravels were perched immediately before the basaltic eruptions that buried them appears to have been close to the main continental divide when the White Hills Gravel was deposited in the early Cainozoic. This restricts the fall site of the meteorite to somewhere on or near this palaeodivide and therefore not far from its final resting-place in the Park Company leases. This is the case regardless of whether the 'reef wash' gravels in which the meteorite was found represent a patch of the White Hills Gravel preserved beneath the basalt, or a younger deposit associated with the early stages of deep lead formation. Such a distinction does, however, affect estimates of the maximum age of the fall. If the reef wash in the Park Company leases represents White Hills Gravel, then the meteorite could be as old or older than late Eocene, based on the time of deposition estimated for the White Hills Gravel by Hughes & Carey (2002). It could have fallen onto the Mesozoic surface that predates the White Hills Gravel before being incorporated into the deposits (Fig. 7). The minimum age of the fall is constrained by radiometric dates for basalts from the Ballarat region, which are between 2 and 4 Ma (Taylor et al. 1996; King 1985). The most representative age of 2.5–3 Ma is for lava from Mt Rowan, a volcano about 4 km to the northwest of the Park Company leases. This eruption point is the most likely

Fig. 5. Possible fragmented schreibersite grain along the interface between main body of fragment and deformed portion, marked by shear-bound etch markings. Field of view is 1.5 mm across.



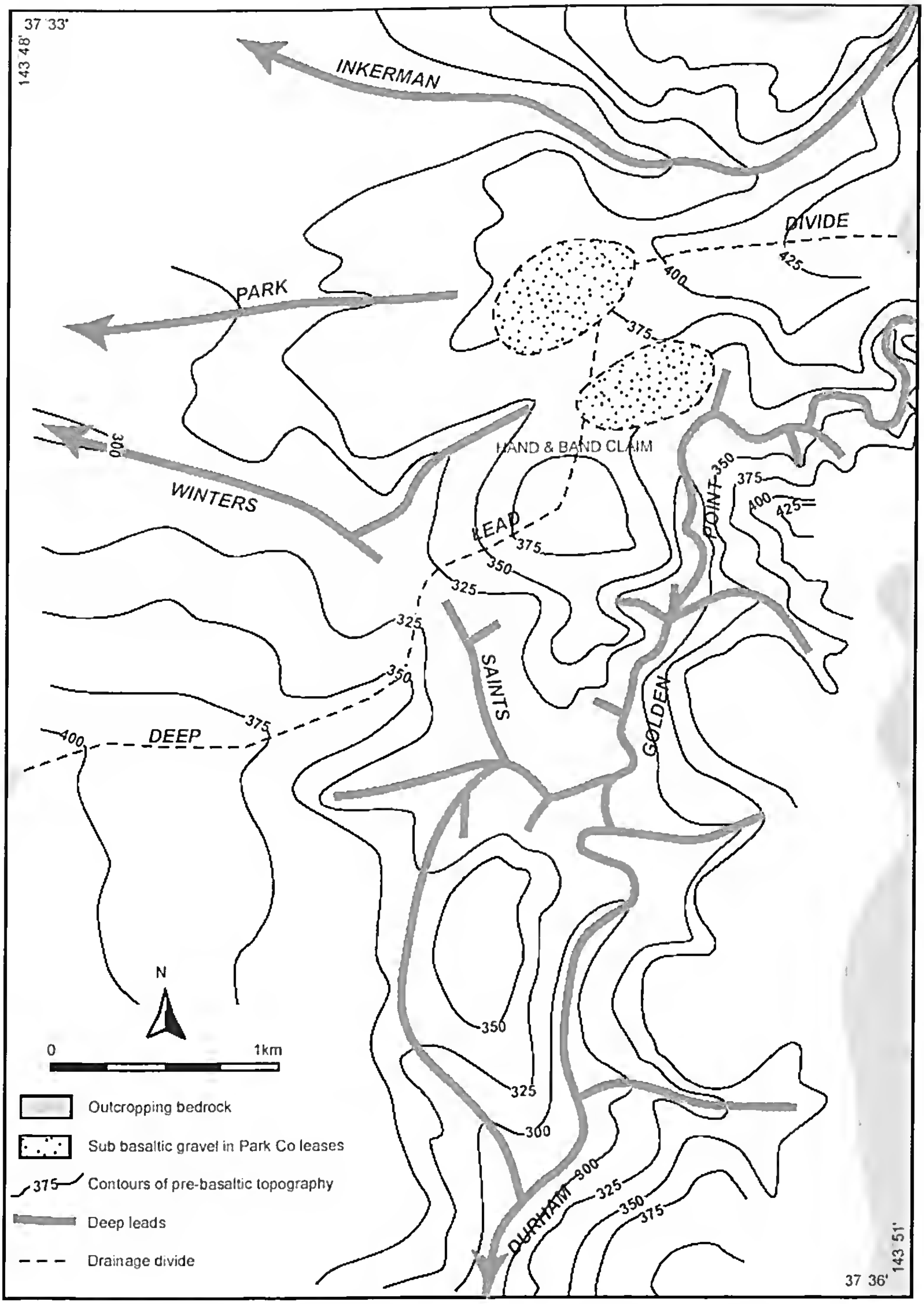


Fig. 6. Reconstruction of the prebasaltic topography in the vicinity of the Park Company leases, modified from Taylor & Gentle (2002). The positions of the areas of gravel wash mined by the Park Company are based on the geological map of Baragwanath (1923).

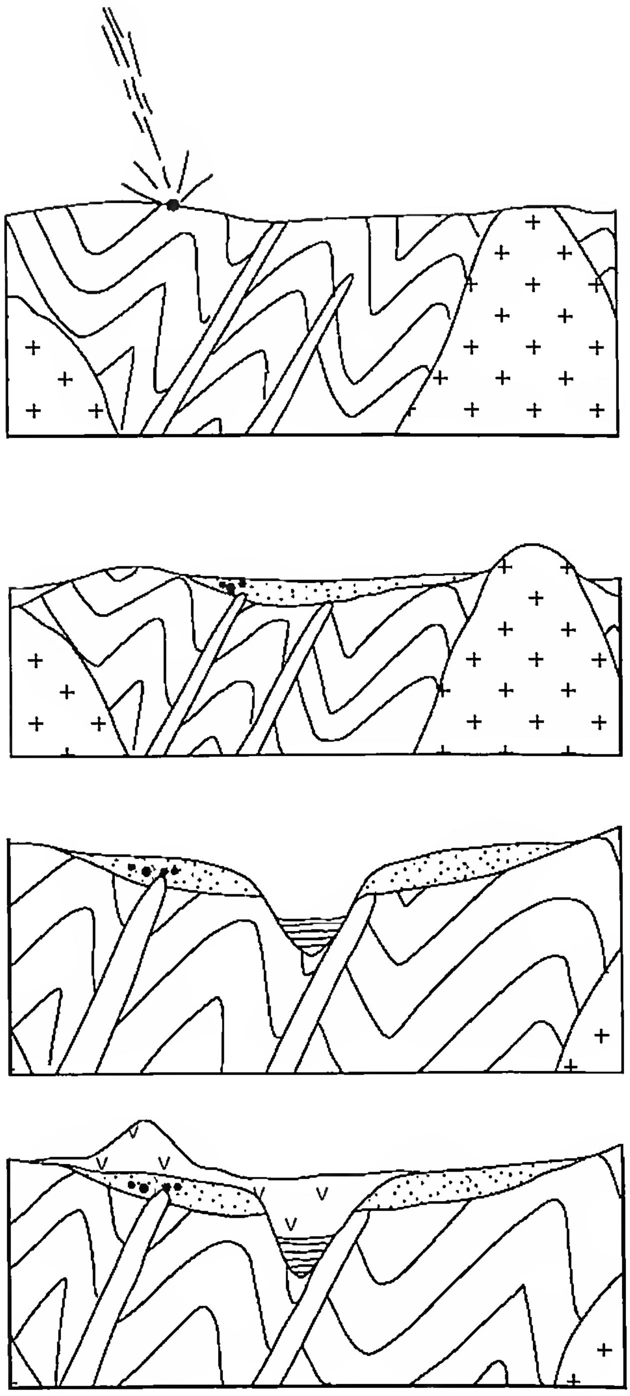


Fig. 7. Possible simplified history of the Ballarat meteorite in terms of the late Mesozoic – Cainozoic landscape evolution in the Ballarat district (after Taylor & Gentle, 2002). Having fallen on the weathered palaeosurface, possibly as early as the late Mesozoic, the meteorite was corroded and broken up during short-distance transport and burial. Subsequently, deep lead valleys were incised through the higher level alluvial deposits. Lava flows (3 Ma) buried these gravels and filled the deep leads.

source of many of the flows that buried the deep leads, including the uppermost flows at Alfredtown, less than 2 km west of the Park Company leases (Fig. 1).

The original size of the meteorite cannot be estimated, but it is likely that the surviving piece is from a much larger mass. At times, the fluvial deposits would have been high-energy environments, as indicated by the abundance of pebbles of massive reef quartz. Under these 'ball-mill' conditions, a relatively coarse-grained iron meteorite would tend to respond to impacts by fracturing along grain or subgrain boundaries, probably weakened by incipient oxidation, with adjacent regions being deformed. Schreibersite grains oriented along subgrain boundaries may have facilitated this fracturing (Fig. 5). Features of the Ballarat meteorite are consistent with such treatment and response.

Once buried by the lava flows, the placer deposits would have been immobilised and conditions would gradually have become reducing, particularly if organic matter was present. The widespread presence of pyrite layers in deep lead gravels indicates they were generally reducing environments. In this situation, a piece of meteoritic iron enclosed in the deposits was likely to survive. The reported presence of other metallic fragments, such as unoxidised copper metal and galena, in the Park Company lead is consistent with reducing conditions.

CONCLUSIONS

While the full circumstances surrounding the discovery and preservation of the Ballarat iron are unrecorded, there are sufficient links between the various strains of evidence to suggest it is a genuine occurrence of a fossil meteorite. It represents a kamacite plate or bundle of plates broken from a coarse-grained octahedrite. The microstructure of partially resorbed Neumann bands and incipient reaction haloes around rhabdite grains is evidence for mild annealing in a low-magnitude, short-lived heating episode.

Sometime before 3 Ma, the precursor mass of the Ballarat meteorite fell close to the main drainage divide in the Ballarat region. Following an unknown period of weathering, the meteorite was caught up in a high-energy fluvial environment that broke it into fragments. These were carried a short distance to be deposited in a placer deposit that was subsequently buried by 3-Ma basalt flows. At least one fragment survived in this environment to be collected during mining operations between 1867 and 1874.

The Ballarat meteorite (IAB) is one of the most common types of iron meteorite, with over 120 known examples. Yet its small size and the circumstances of discovery make it highly unusual. It is the smallest iron meteorite known from Victoria, supplanting Wedderburn (30 g) found about 125 km to the north of Ballarat in 1951. Possibly the only smaller iron meteorite known is Castray River, from Tasmania, with a total mass of about 10 g (Bevan, personal communication).

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TRANSACTION

OF THE

ROYAL SOCIETY OF VICTORIA

LECTURE TO THE DANISH CLUB
18th September, 2003
by Phillip Law

I accepted the invitation to lecture here tonight – a very rare acceptance – because I wanted to pay a tribute to the part played by Denmark in the development of Australia's role in Antarctic affairs.

At a time when Australia's plans to establish a permanent station in Antarctica were stalled through lack of a suitable ship, Denmark provided the answer to the problem in the form of a small icebreaker "Kista Dan". In December 1953, her departure from Melbourne with the pioneer Mawson party marked the beginning of a 34-year association with the Danish shipping company "J. Lauritzen" from which we chartered, in succession, four ships.

I was honoured to become a friend of the head of the company – Knud Lauritzen – who on several occasions entertained me and my wife Nel during our several visits to Copenhagen. One entertainment was particularly memorable. Our visit coincided with a visit to Copenhagen by the Royal Covent Garden Ballet Company from London. Lauritzen had arranged a bay cruise for the ballet dancers on board the company's small training sailing barque "Lilla Dan" and had invited Nel and me to join them.

It was a perfect warm, sunny day. We sailed along, sunning ourselves on deck and partaking of oysters, prawns, crayfish and champagne. A piano accordian player provided jazz music and the ballet dancers jived enthusiastically. It was really magic!

SOME ANTARCTIC LEADERS

When one comes to look at what has been written about the history of Antarctic exploration, one is not very impressed. The trouble is that certain patterns of thought concerning Antarctic events become widely established as a result of the media's portrayal of them and the effect of such portrayal upon the general public. Long before some historian comes along to write up the events, they

have become enveloped in shrouds of ignorance, error, emotion, sentimentality, chauvinism and exaggeration.

Tonight I look back on the history of Antarctic exploration to compare the accomplishments and leadership qualities of some of the world's great Antarctic expeditioners and, in doing so, to show how their reputations confirm my opening statement.

Those I shall discuss are Scott, Shackleton, Amundsen and Mawson.

But first, I should like to stress the difference between discovery and exploration. Discovery, in the Antarctic context, is seeing geographical features for the first time. Exploration, in that context, is describing the features, and accurately determining their locations so they can be mapped. This is a most important distinction and one that, unfortunately, has seldom been made.

In assessing the accomplishments of these men, I shall use four criteria :

i) what they, personally, explored and discovered;

ii) what the men under their leadership achieved;

iii) their leadership qualities; and

iv) the foundations for future accomplishments that they laid down and their ongoing influence upon later generations.

I shall deal with them chronologically.

Robert Falcon Scott led two expeditions, in 1901-04 and in 1910-13. Both were in the Ross Sea sector. His exploration forays were only 300 miles in extent, according to the historian J. Gordon Hayes (1928). However, he and the men of his two expeditions discovered about 1300 miles of coast, mainly in the N.Z. sector.

Note how little was explored. It is comparatively easy to discover features. You can, for example, sail along a cost, 40 miles off-shore, and make notes of mountains, bays and capes that you observe.

Exploration is more difficult. You must land and survey the features, accurately determining their exact positions (generally by astronomical observations).

Scott's scientific results were extensive, with many volumes of scientific reports covering a variety of disciplines. They were uniquely valuable because in many subjects they provided the first information ever gained in the Antarctic and opened up various avenues for research by later expeditions. The high standards achieved were due to the quality of the scientists that were included in his teams.

However, despite these accomplishments, Scott has been widely criticized. Errors in planning, combined with rare bad luck, led to the deaths of the five men in his South Pole party. He was autocratic and reluctant to accept advice or to consult others. He was an amateur who lacked experience in field work and made no attempts to prepare himself for Antarctic conditions either by previous activity in the frigid regions of Europe or research of available literature.

During some eighty-odd years of searching for the NW passage and a route to the North Pole, the Royal Navy had despatched more than 30 expeditions. The experience gained from these covered man-hauling, dog-sledging, food, scurvy, and survival procedures. Captain Scott, R.N., did not bother to read the extensive material available in the Royal Navy archives and repeated many of the mistakes that these early Arctic explorers had made.

Yet the tragic story of Scott's fate, with its engrossing examples of endurance and fortitude, did more to stimulate adventure in young people and later Antarctic endeavour than probably any other narrative in the British language. And the emotion that his fate evoked led to an appeal for funds that resulted in support for later explorers and, more important, to the establishment of the Scott Polar Research Institute in Cambridge, a world-renowned institute.

So, all in all, I rate Scott very highly overall, but not for his personal exploration, which was not very much.

The Shackleton saga is quite a different one. Contrary to general opinion, Shackleton's life was a succession of failures if regarded from the point of view of his objectives. He accompanied Scott on his first attempt to reach the South Pole in 1903, and, stricken with scurvy, spent part of their retreat being carried on a sledge. He was shipped back to England and missed the second year of the expedition.

On Shackleton's 1907-09 expedition he was forced to abandon his own attempt to reach the Pole when, according to his records, he was within 96 miles of it.

His third expedition, 1914-17, failed when his ship Endurance was crushed by pack ice before he had reached the Continent. And on his final expedition, 1921-22, he died at South Georgia before proceeding into Antarctic waters.

In addition to all this, Shackleton embarked upon a number of get-rich-quick gold mining financial ventures, each of which failed.

He, himself, explored very little, his main achievement being pioneering the Pole route via the Beardmore Glacier. He explored a stretch of terrain

about 200 miles in extent during his 1907-09 expedition.

His men, however, achieved much more. David, Mawson and McKay made a sledge journey of 1200-odd miles to reach the South Magnetic Pole, during which Mawson surveyed in detail about 200 miles of the west coast of the Ross Sea. Shackleton, in his ship, explored the edge of the Ross Ice Shelf. Hayes awards Shackleton 300 miles of exploration and his expedition 1035 miles of discovery.

Scientifically, Shackleton's 1907-09 expedition was productive for, like Scott, he had a fine team of scientists. The output for this one expedition was somewhat less than half of that of Scott's two expeditions.

Shackleton was a democratic leader, in an era when leadership was almost universally autocratic, and this, with his extrovert and magnetic personality, gained him the loyalty and affection of his men. As a leader in the field, he was outstanding.

The Shackleton story, like Scott's, had a profound effect upon generations of young and old, his survival and his leadership, following the destruction of his ship *Endurance*, being one of the greatest narratives of British adventure. It is largely upon this that his fame rests, and for this he scores well under criterion four.

As an interesting footnote to all this, Sir Douglas Mawson once told me that he believed Shackleton faked his travel records and that he could not have reached a point 96 miles from the Pole. Mawson based his judgement upon his own experience of man-hauling a sledge for 1200 miles. The "Grey Eminence" of 19th Century British polar exploration, Sir Clemence Markham, expressed the same view, challenging the daily distances traversed, particularly in ascending the Beardmore Glacier.

Several years ago in England, a descendant of a man who accompanied Shackleton on this sledge journey, released the diary of this man, which specifically states that the Boss, as he was called, cribbed a few miles each day when he entered up his travel log!

All in all, I rate Shackleton as a very great adventurer, but not much of an explorer, and I do not give him nearly as many marks as Scott.

Now consider Amundsen. Whereas Scott and Shackleton were amateurs, Amundsen was highly professional. He had spent twenty or more years preparing himself for his conquest of the South Pole. He had gained Antarctic experience when, as second mate, he wintered on De Gerlache's ship, the *Belgica*, which was beset for the winter in Antarctica in 1898. He studied for, and gained, his Master's ticket and was experienced in skiing and dog sledging. Further, he had carefully studied the exploits of that great Polar traveller, Fridjhof Nansen.

Amundsen's route to the Pole, via the Axel Heiberg Glacier, was steeper, more crevassed and much more difficult than that of Scott up the Beardmore, as Wally Herbert, a British expeditioner, demonstrated, shortly after the IGY, when he drove a dog team down it. Yet Amundsen reached his goal and returned with a minimum of fuss. The main criticism of his expedition is that he did no exploration, i.e. surveying, as he went along, so little in fact, that it is even difficult to plot accurately the route he took. The real exploration of the Axel Heiberg Glacier and its environs was not carried out until the IGY, more than 50 years later.

Nor did Amundsen's party carry out any scientific work. His journey was essentially a rapid dash to reach a defined goal, nothing more. Hayes says of it: "It practically was wasted work, because no proper cartographical record was made, even of the bare route; whereas there was ample (dog) power, food and time to have explored the Queen Maud Range and Carmen Land. Amundsen should have taken at least one competent surveyor on his Polar journey; for it is really no use breaking the first trail unless something tangible is done to open up the new country".

Hayes quotes the extent of new land discovered (but not explored) as 1300 miles, although Amundsen logged 1612 miles of actual sledging.

It is ironical that, in the Arctic, Amundsen's record as an adventurer, a discoverer and an explorer is at the highest level; it was he who discovered – and charted - the North-West Passage!

Even he had his critics when it came to leadership. Loyal to his friends, he could be quite vindictive if opposed. When returning to his base from an abortive early attempt on the South Pole route, which he began too early in the Spring, he deserted his party and raced on ahead. As a result, two sledge groups nearly failed to reach base. One man, Johannsen, bitterly rebuked him after returning. Amundsen regarded this as mutiny, removed him from the final assault party, and ostracized him for the rest of the expedition. Shamed and humiliated, the man later, in Norway, committed suicide.

Rated accordingly to my four criteria, Amundsen does not score a high total in Antarctic endeavour, although like Shackleton, he gets high marks as an adventurer.

Moving on now to Mawson, we find a large mile-

age for personal exploration if we include his long magnetic pole journey while serving with Shackleton. In his AAE and BANZARE expeditions, the total for personal exploration is only about 300 miles, for on his second expedition, BANZARE, he achieved practically no personal exploration. He made only three landings in two summer voyages and made no cartographic observations on any of them.

In miles of coast discovered, he rates far more highly, with around 1800 miles to his credit, for his BANZARE voyages sighted stretches of previously unknown coast while passing by, out to sea.

Mawson's scientific results were extensive, with observations in various disciplines from Macquarie Island, Commonwealth Bay, the Western Base on the Shackleton Ice Shelf, and marine biology and oceanography during the BANZARE voyages.

As a leader, Mawson rates more highly than Scott and Amundsen. First, his style was more democratic and, second, he was himself a scientist and thus was able to relate better to the scientists under his command. Also, he personally ensured a high priority for all the scientific work and worked hard later to see that the results were published.

With reference to criterion number four, it can be said that Mawson's influence was great. His work has been an inspiration to numerous young adventurers in Australia while, in an ongoing role, his was the major influence in persuading the Commonwealth Government in 1947 to establish the ANARE. In the early days of my expeditions, while serving on the ANARE Executive Planning Committee, he was a powerful supporter of my plans and programs.

Hayes has this to say of him :

"Sir Douglas Mawson's 1911-13 expedition may be held up as a model for others to copy. Its excellence lay in its design, its scope and its executive success; and it owes its exalted position among other Antarctic expeditions mainly to the fact that it was originated and conducted by scientists of administrative ability who are the fit and proper persons for such undertakings. Reason appears to have ruled throughout."

I have also applied my criteria to other Antarctic leaders. I should have liked to discuss Richard Byrd (USA), Finn Ronne (USA), John Rymill (Australia), Vivian Fuchs (UK), Edmund Hillary (NZ), Mikhail Somov (Russia) – for no analysis of Antarctic endeavour would be adequate without examining their work, but time does not permit.

You should understand that the four expeditions I have treated provided merely an introduction to the opening up of the last unknown continent. Extensive exploration of Antarctica did not occur until the years 1950-70, particularly during the International Geophysical Year (1957-58) and the years that followed. Australians figured prominently in this work, discovering vast tracts of unknown country and exploring in detail more than a million square kilometres of terrain. One ANARE man, surveyor Syd Kirkby, has explored more than the explorations of Scott, Shackleton, Amundsen and Mawson combined! His is a remarkable record.

He was the wintering surveyor at Mawson in 1956 and 1960 and returned in 1980 as Station Leader and surveyor. He accompanied me on summer voyages of exploration in 1955-56, 1956-57, 1960-61 and 1962-63. He was the hands-on explorer, the man who actually surveyed and mapped the country.

His surface exploration – by dog sledges, weasels and tractor trains – covered 1200 km of "new" territory. His actual travel distances are much greater. The lengths of coastline he explored with me, i.e. coasts where no-one had been before, totalled 3000 km.

By air, during exploration flights and flights to achieve first landings, he covered approximately 3000 km. His astrofixes range from 44 degrees E to 167 degrees E longitude and inland to the most southerly nunataks of the Prince Charles Mountains.

No other person, living or dead, has done so much!

The IGY and the years that followed produced accomplishments by a number of remarkable men whose exploits have received no wide acclaim. I remember particularly Americans Crary and Bentley and Russians Somov and Kapitsa. I have been urging for years that more comprehensive histories of Antarctic exploration should be carried out, dealing with the major explorations of the years 1950-70 and omitting the work of the heroic era, which has been rehashed time after time and is still attracting the attention of book authors.

My own judgement, ranking all the men I have mentioned, according to the criteria I stated at the beginning, is that Scott, Mawson, Byrd and Fuchs are well ahead of the rest. However, what is needed is a modern J. Gordon Hayes to survey the whole panorama of Antarctic history in detail. Only then will Antarctic exploration be presented to public view in its true perspective.

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non *Eudendrium generale.*—Watson 1982: 89, pl. 10, fig. 3.

Eudendrium lendenfeldi Briggs 1922: 150.—Rosler 1978: 104, 120, pl. 20, figs 1-3.

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CURTIS, N. P., 2001. Germination of *Xanthorrhoea australis* using treatments that mimic post-fire and unburnt conditions. *Proceedings of the Royal Society of Victoria* 113(2): 237-245.

BERGSON, H., 1928. *Creative Evoltion.* MacMillan and Co., Limited, London, xv+425 pp.
ROSEN, B.R. & TURNŠEK, D., 1989. Extinction patterns and biogeography of scleractinian corals across the Cretaceous/Tertiary boundary. In *Proceedings of the Fifth International Symposium on Fossil Cnidaria including Archaeocyatha and Spongiomorphs*, P.A. Jell & J.W. Pickett, eds, Association of Australasian Palaeontologists, Brisbane, Queensland, 355-370.

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